

Understanding the cephalic eyes of pulmonate gastropods: A review*

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Abstract: This review showcases one group of gastropod's ability to perceive light through the eyes. The central question is simple: what are the visual performances and tasks of cephalic eyes in gastropods? That topic in itself is rather broad and is here applied to pulmonate gastropods, coming from terrestrial and aquatic biomes as well as different habitats and microhabitats, exhibiting different life-styles and light-tolerances. Therefore, the main objectives have been to analyze (1) anatomical and ultrastructural eye characteristics, (2) optical systems, (3) image-forming capabilities and possible functional consequences of eye size and design, (4) interactions between gastropods and their environment mediated by the visual information obtained through the eye, and (5) the specific visual tasks that the eyes serve. During the course of this study, a range of variations (= adaptations) in both optical and retinal design parameters, including eye size, aperture size, quality of optical image, retinal shape, sampling density, and optical sensitivity were discovered. All species of pulmonate gastropods studied have paired simple camera-type eyes that operate with advanced fixed focal-length optics. However, in terrestrial snails and slugs as well as freshwater limpets, the optics cannot produce a focused image on their shallow retinas. This seems to indicate that eyes in these species are not designed to receive a focused image and are likely to measure only the average light intensity or quality over large angles rather than resolve fine image details. The aquatic snails examined are able to focus a sharp image on the photoreceptive layer of the retina due to the deepening of the latter (at least in a localized region). Although there is a significant correlation between specialization of the eye (e.g., quality of optical image, sensitivity, and resolution) for a particular visual task in a specific habitat that the species encounters, there is no correlation between cellular composition of the retina and light/dark preferences. Their high optical sensitivity allows terrestrial snails to perform the necessary visual tasks in both bright and dim light, whereas the eye in aquatic species functions preferentially under bright light conditions. In conclusion, pulmonate gastropods use their eyes primarily for the following two kinds of visual tasks: (1) discriminating objects and possible enemies in their environment and (2) monitoring the environmental brightness level to orient towards dark places. The first type of visual task is characteristic of the aquatic snails and is served by image-forming eyes; the second is typical of terrestrial snails and slugs and is best served by a blurred image. Attention is given to visual ecological adaptations, specific visual needs, and the evolutionary history of gastropods.

Key words: vision, eye optics, visual behavior, retina, molluscs

The literature dealing with invertebrate eyes is extensive and especially with regard to molluscs, includes excellent reviews on photoreceptor evolution (Eakin 1968, Salvini-Plawen and Mayer 1977, Vanfleteren 1982), comparative anatomy and optics (Land 1981, 1984, Land and Fernald 1992), and phototransduction and physiological mechanisms (Messenger 1981, 1991, Nasi *et al.* 2000). The most recent books by Land and Nilsson (2002) and Warrant and Nilsson (2006) represent a comprehensive account of all known types of eye and provide an up-to-date synthesis of our current knowledge of invertebrate vision. However, even in these latest publications, pulmonate lineages, reviewed more than 30 years ago by Kerkut and Walker (1975), are somewhat under-represented. Moreover, most of the conclusions on the importance of eyes and vision in pulmonates stem from just a handful of species, and of them the terrestrial snails belonging to the genus *Cornu* (Born, 1778) alone have attracted the bulk of attention. This, no doubt, was the

result of the sustained, detailed, and elegant anatomical and ultrastructural examinations of the *Cornu aspersum aspersum* (Müller, 1774) eye by Eakin and Brandenburger and their colleagues (e.g., Eakin and Brandenburger 1967a, 1967b, 1970, 1975a, 1975b, 1982, Brandenburger and Eakin 1970, Eakin and Ferlatte 1973, Brandenburger 1975, Brandenburger *et al.* 1976) as well as some early electrophysiological studies by Berg and Schneider (1967), Gillary (1970), Pasic *et al.* (1974), and Berg (1978). The present review deals with the cephalic eyes of gastropods generally, and in pulmonates in particular, focuses on eyes of various sizes, differences in retinal design, and the extent to which their optical equipment permits image formation. Some of our recent observations, together with those of other researchers, will be briefly summarized.

For more than fifteen years we have been studying the eyes of pulmonate gastropods, and in this paper we shall review what is known of the morphology and ultrastructure

* From the symposium "Molluscan models: Advancing our understanding of the eye" presented at the World Congress of Malacology, held from 15 to 20 July 2007 in Antwerp, Belgium. Co-sponsored by the National Science Foundation and the American Malacological Society.

of their retinal cells. We shall discuss recent comparative anatomical and ultrastructural findings and results based on behavioral tests and investigations that have involved optical modeling. We will evaluate some of the new ideas that arose from analyses of morphological and ecophysiological adaptations to terrestrial and aquatic ways of life and will give possible reasons for the large variety of retinal designs and optical systems one encounters in the pulmonate eye. Special emphasis is given to the research of the authors and their associates.

ANATOMY

With the exception of a few subterranean stylommatophoran forms (e.g., *Cecilioides acicula* (Müller, 1774) and *Helicodiscus singleyannus* (Pilsbry, 1889) as well as some blind *Ellobiacea* (Grassé 1948), all pulmonates have a single pair of eyes located on the head. The position of the eyes in relation to the tentacles is frequently employed as a taxonomic criterion. In stylommatophoran land snails and slugs, as well as in systellommatophoran marine slug-like pulmonates, eyes are developed at the tips of the mobile, retractile tentacles. In freshwater basommatophoran snails and limpets, the eyes are located medially or laterally at the base of a single pair of mobile tentacles close to the cerebral ganglion. Each cephalic eye consists of a cornea, a lens, a vitreous body, a non-inverted retina, the eye capsule, and the optic nerve.

The plane of the bilateral symmetry of the cephalic eyes coincides with the dorso-ventral plane of the heads in *Lymnaea stagnalis* (Linnaeus, 1758), *Radix peregra* (Linnaeus, 1758), *Planorbarius corneus* (Linnaeus, 1758), and *Physa fontinalis* (Linnaeus, 1758) and with the ventro-lateral plane in species with an accessory retina; no preferred plane is demonstrable in the remainder of the terrestrial pulmonates.

Integument

In all of the investigated pulmonates the eyes are placed under a circular area of a specialized region of the integument, that at this location is thin, unpigmented, dome-shaped, and translucent. The function of the integument layer may be a protective one, reducing possible mechanical injury and desiccation, the latter presumably of importance for terrestrial and some aquatic molluscs that lead moderately amphibious lifestyles. The integument may also be involved in regulating osmotic and ionic processes, since aquatic species in particular have to continually osmoregulate, while terrestrial gastropods need to minimize water loss.

Perioptic sinus

Willem (1892) described a spacious blood lacuna, the perioptic sinus, from the region around the eye of *Lymnaea stagnalis*. Later, Stoll (1973) confirmed Willem's observa-

tions in the same species and Bobkova *et al.* (2004a) described the perioptic sinus in *Radix peregra*, *Physa fontinalis*, and *Planorbarius corneus*. The observations showed that the sinus is anatomically isolated from the rest of the hemocoel and connected to it only through the interstitial tissue.

It is well known that sinuses, located in strategic regions, may become cavities of the hydrostatic skeleton, with blood serving as the hydrostatic fluid. In terrestrial species, however, the situation is different; the blood cavity in the retractable optic tentacles together with the hemocoel may function as a hydraulic rather than a hydrostatic system. We suggested (Bobkova *et al.* 2004a) that freshwater basommatophora actively place their eyes into the perioptic sinus, firstly, in order to fix their rigidly-held eyes in a particular position with regard to the body, and, secondly, to minimize the risk of possible mechanical compression when the animal withdraws its body into the shell. However, limpets like *Latia neritoides* (Gray, 1850) and *Ancylus fluviatilis* (Müller, 1774) apparently do not have the perioptic sinus (Meyer-Rochow and Bobkova 2001), but at the same time, these species have cap-like shells and do not have to compress their body as much as, for example, *Lymnaea stagnalis*.

Basal lamina and eye capsule

The retinal cells rest on a basal lamina. The lamina separates the retina and eye capsule as well as the cornea and interstitial tissue or, as in some aquatic species, cornea and lumen of the perioptic sinus. The basal lamina is continuous throughout its length and of constant thickness. Both the basal lamina and eye capsule continue into branches of the optic nerve. Along the course of the nerve, the capsule is then gradually replaced by a sheath of glial cells as, for example, in *Lymnaea stagnalis* (Bobkova 1998).

The eye capsule consists mainly of striated collagen fibrils and a layer of muscle cells. The muscle cells are embedded circumferentially (except for the area of the cornea) into an amorphous matrix to which they are attached by hemidesmosomes (e.g., *Cornu aspersum aspersum*: Eakin and Brandenburger 1972; *Lymnaea stagnalis*: Bobkova 1998). The muscles are innervated by fine neurites, containing cored vesicles. The source of these neurites has still not been clearly determined. Recently it was demonstrated by immunohistological means that the eye capsule receives serotonergic innervation (Zhukov and Tuchina 2008).

Retinal design

As a rule, the eyes of all pulmonates studied to date possess conventional, cup-shaped retinas (e.g., *Cepaea nemoralis* (Linnaeus, 1758) and *Trichia hispida* (Linnaeus, 1758): Fig. 1A-B). The eyes of some freshwater pulmonates such as *Lymnaea stagnalis*, *Radix peregra*, *Physa fontinalis*, and *Planorbarius corneus* have retinas that are portioned into

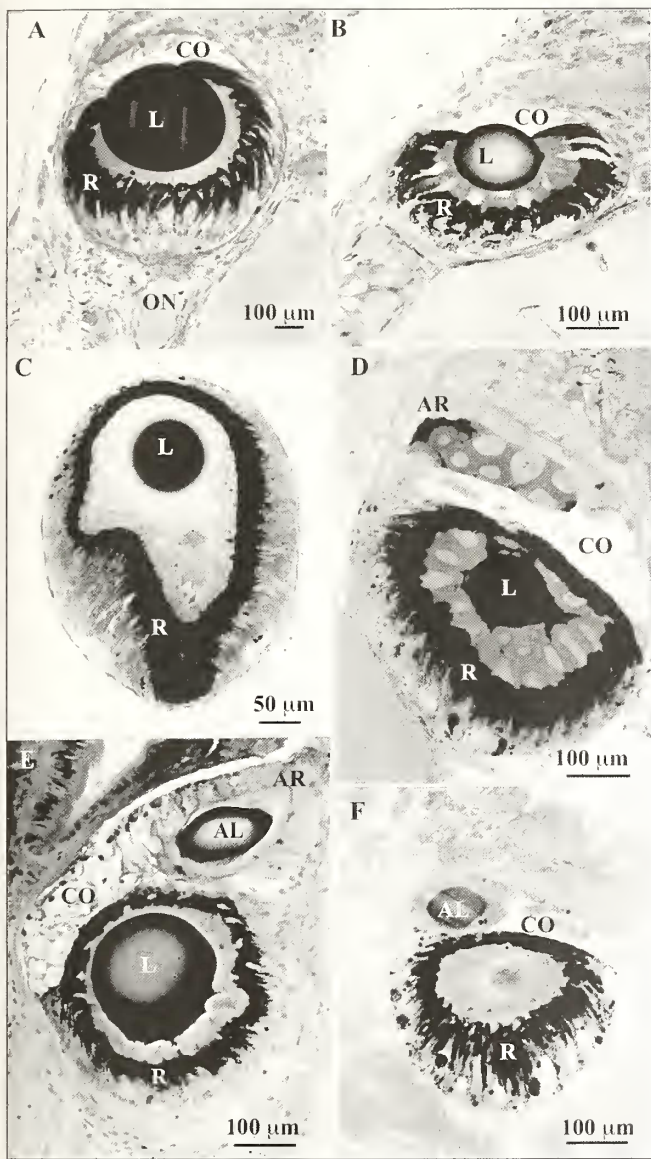


Figure 1. Light micrographs of longitudinal sections of camera-type eyes of various designs in pulmonate gastropods. (A) *Cepaea nemoralis*, (B) *Trichia hispida*, (C) *Lymnaea stagnalis*, (D) *Deroceras agreste*, (E) *Achatina fulica*, and (F) section through lens of additional eye in *Deroceras agreste*. AL, additional lens; AR, additional retina; CO, cornea; L, lens; ON, optic nerve; R, retina. A, B, and C from Bobkova *et al.* 2004a; D and F from Bobkova *et al.* 2004b with permission of John Wiley and Sons, Inc.

dorsal and ventral depressions (termed “pits”) (Fig. 1C). The pits are separated by an internal ridge, called a “crest”, and based on their pigmentation, can be seen *in vivo* (Bobkova *et al.* 2004a). Of all non-pulmonate gastropods, only the opisthobranch *Navanax inermis* (Cooper, 1863) possesses an eye with a “bi-lobed” lens and a non-hemispherical retina (Eskin

and Harcombe 1977). However, the question of whether this lens can produce an image on the retina has not been examined. Four distinct retinal layers in the eyes of gastropods can be distinguished, namely the microvillar, the pigmented, the somatic, and the plexiform layer.

Additional photoreceptive structures

Some pulmonates have a double eye. The additional photosensory organ was first described by Henschman (1897) in the slug *Limax maximus* (Linnaeus, 1758). The terrestrial snail *Achatina fulica* (Férussac, 1821) also has an additional retina (termed “accessory” by Tamamaki and Kawai 1983), invariably equipped with its own lens and an anatomically separate retina from that of the main eye (Fig. 1E). In *Limax flavus* (Linnaeus, 1758), Tamamaki (1989) found traces of a lens and a discontinuity of the two optic cavities. Therefore, we suggest calling the structure in question “an additional eye” rather than an “additional retina” or “accessory retina”. Moreover, we have demonstrated that the cornea and the additional eye with its own nerve in the snail *A. fulica* may regenerate separately from the main eye (Bobkova *et al.* 2004b). But what we do not know is if such a regenerated structure is a functional organ.

The slug *Agriolimax reticulatus* (Müller, 1774) (Newell and Newell 1968) possesses an additional retina but lacks the additional lens, while *Deroceras agreste* (Linnaeus, 1758), also a slug, possesses both an additional retina and an extra lens (Fig. 1D, 1F). The additional lens can easily be isolated from its cavity. The lens is irregularly shaped and the vitreous body of the additional retina is continuous with the vitreous body of the main eye in *Deroceras agreste* (Zieger *et al.* 2008). Thus, we accept the term “additional retina” for species of pulmonates in which a vitreous body, associated with the additional retina, is continuous with vitreous body of the main eye, but we use the designation of “additional eye” when a discontinuity of the two optic cavities is present.

On the basis of the work by Tamamaki and Kawai (1983) on the eye of *Achatina fulica*, Newell and Newell (1968) on *Agriolimax reticulatus*, Tamamaki (1989) on *Limax flavus*, and us on *Deroceras agreste* (Zieger *et al.* 2008), it has become clear that the cellular composition of the additional retina is similar to that of the main eye. However, there are no screening pigment granules in the supportive cells of the additional retina. Neurosecretory cells were absent as well. The photoreceptor cells in the additional retina are large and their dome-shaped apices bear well-organized (regular), long microvilli. Accumulations of photic vesicles are also present, but the latter are not as tightly packed as those of the photoreceptors of the main retina. The microvilli were observed to be aligned in perpendicular orientations (Fig. 2), but we could not provide any morphological evidence for the view that the perpendicularly oriented mi-

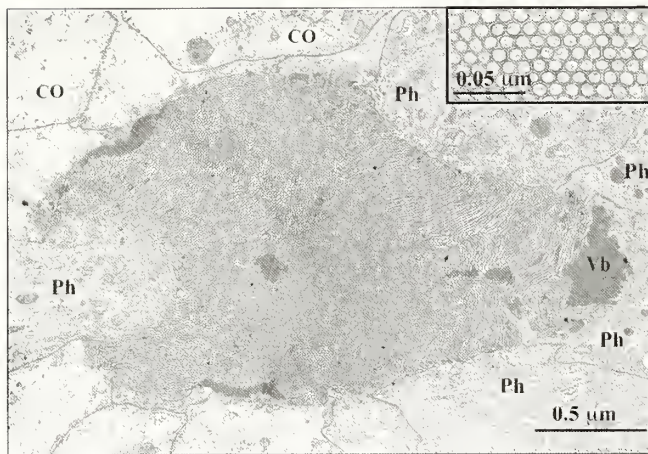


Figure 2. Electron micrograph of additional retina in *Deroceras agreste*. The inset shows a transverse section through the presumably light-sensitive microvilli. CO, corneal cells; Ph, photoreceptor cells; Vb, vitreous body. From Zieger *et al.* 2008 with permission of John Wiley and Sons, Inc.

crovilli might belong to neighboring (different) photoreceptor cells (Zieger *et al.* 2008).

As to the function of the additional retina, two theories have been proposed: (1) perception of changes in the intensity of the ambient light and (2) perception of infrared radiation. The latter could not be confirmed experimentally, but it has not been possible either to demonstrate that the additional eye is a visual organ at all. Moreover, the lack of screening pigment permits light to reach the presumed photoreceptor cells from any direction, making image formation impossible. However, Newell and Newel (1968), observing the behavior of *Agriolimax reticulatus* in a state with partially retracted optic tentacles, concluded that the additional eye would become exposed to light when the aperture of the main eye becomes fully masked by the pigmented integument. Therefore, the additional eye may be useful in situations like the partially retracted tentacle (Tamamaki 1989).

The hypothesis that in *Deroceras agreste* the additional retina could play a role as a sensor of polarized light had to be rejected as a consequence of carefully conducted behavioral tests (Vakoliuk 2005). Although we did not evaluate the optical system of the additional retina in *D. agreste*, we are nevertheless convinced, for reasons explained above, that it cannot form an image, even if it should turn out to be a functional light sensor.

The plexiform layer

The plexiform layer in all pulmonates studied to date is formed by axons of both photoreceptive and neurosecretory cell types (e.g., Brandenburger 1975, Eakin and Brandenburger 1975b, Kataoka 1975, Eakin *et al.* 1980, Katagiri *et al.*

1995, Bobkova 1998, Meyer-Rochow and Bobkova 2001, Bobkova *et al.* 2004a). As shown for *Lymnaea stagnalis* (Bobkova 1998), the axons of the photoreceptor cells may be joined by synapse-like contacts of two morphological types. The first we call “invagination”, for in this type the membrane of one axon drives a narrow finger-like protrusion into the other axon. Such contact seems to be very effective, as in the case of sensory cells in vertebrate electroreceptors of the “Lorenzini Ampoule” in skates (Byzov 1994). The second inter-axonal contact type in gastropods belongs to the flat “*en passant*” type.

The ultrastructure of synapses in the plexiform layer of the eye in *Lymnaea stagnalis* appears similar to the structure in the gastropod central nervous system. From studies in the snail *Achatina fulica*, it appears that there are at least two morphological types of synapses: (1) asymmetrical, or polarized, synapses with vesicle aggregation on one side of the active zone and (2) symmetrical synapses, with vesicle aggregations and pre-membranous densifications present on both sides of the synaptic cleft, thus indicating bi-directional transmission across the junction (cf., review by Chase 2002).

We suggest that contacts of both types can possibly provide summation of signals from groups of neighboring photoreceptors. Summation increases the number of photons received per channel during periods of low luminance. Such a strategy is employed by several other animals but only at the expense of spatial resolution (Seyer *et al.* 1998).

Organelles of great interest in the eye of *Lymnaea stagnalis* are the numerous small, clear, and dense vesicles. They are abundant close to the photoreceptor axonal membrane in the extracellular space (Bobkova 1998). Morphologically identical pictures of them were taken from the extracellular space in the CNS of *Cornu aspersum aspersum* (Chalazonitis 1971) where such vesicles were associated with exchanges of macromolecules between adjacent neuronal axons, axons and glial cells, and neurons and axons. We presume that the axons of the photoreceptor and possibly neurosecretory cells may have a metabolic link at the level of the plexiform layer. This process might be related to cell respiration because vesicles have been observed only in the peri-membrane portion of the axoplasm and in the intercellular spaces. The osmiophilic material in the vesicles can be one of the metabolic products of respiratory pigments like hemocyanin, which is known to function extracellularly.

Connections to the central nervous system

The axons of the retinal photoreceptors pass out of the eye by way of the optic nerve and form connections with second order neurons in the cerebral ganglion of the central nervous system. As demonstrated for *Lymnaea stagnalis* and *Planorbarius corneus*, afferent information from the eyes is widely distributed throughout the CNS. Nerve fibers, start-

ing in the ipsilateral optic nerve were traced through the cerebral ganglion to the contralateral optic nerve, suggesting tight interactions between the two eyes (Zhukov and Tuchina 2008). Optic tract projections were found to end on the hair cells of the statocyst in *Lymnaea stagnalis*. The animal initially responds to light with phototactic behavior and moves towards the light, but in response to mechanical turbulence it clings to the surface. Such paired visuo-vestibular conditioning results in conditioned escape behaviors (cf., review by Sakakibara 2006).

Efferent innervation of the eyes occurs as well. Efferent fibers from the CNS form a varicose plexus within the eye capsule in *Lymnaea stagnalis* and *Planorbarius corneus* (Zhukov and Tuchina 2008). Serotonergic efferent fibers influence the amplitude of the electroretinogram and change absolute sensitivity to light in *Lymnaea stagnalis* (Zhukov *et al.* 2006).

OPTICAL SYSTEM

The optics of the eyes of gastropod molluscs vary greatly and range from a pigmented pit without a lens to sophisticated eyes with hard spherical lenses and image-forming capacity (Land 1984). According to Messenger (1981), the advanced cephalic eyes present in pulmonates can be classified as a “closed vesicle, camera-type eye”, capable of forming an image on the retina (Nilsson 1989). However, such a categorization suggests a certain degree of homogeneity within the taxon but provides little information on possible modifications and/or variations of the optical system as well as the visual adaptations seen in gastropods.

Based on numerous pulmonate species examined by us (Bobkova *et al.* 2004a, 2004b), we now conclude that the positions or shapes of the lenses have evolved to become optimized in different environments as a response to the prevailing light conditions. Muscular or other connective tissues attached to the lens were not seen, and no kind of membrane or sheath delineating the lens appears to have developed. For the terrestrial snail *Cornu aspersum aspersum* it has been suggested that the shape of the eye could be changed through the actions of the musculature of the eye capsule and associated capsular strands (Mortensen and Eakin 1974). However, no experimental proof for this view has ever been presented. Based on our own observations, Bobkova *et al.* (2004a) concluded that pulmonates have a fixed focal-length optical system and a total absence of accommodative ability. The main components of the optical system in all of the pulmonates studied until now are the cornea and the lens.

Cornea

The convex-concave cornea represents the most anterior part of the eye vesicle. In terrestrial snails it is much

thicker than that of the aquatic species (e.g., in molluscs with comparable eye sizes like *Trichia hispida* and *Radix peregra*, the thickness of the cornea at its center is about 13 and 3 μm , respectively) (Bobkova *et al.* 2004a). Yet, despite the difference, comparisons of the corneae of the eyes of terrestrial (e.g., the slug *Limax flavus*: Kataoka 1977, the snail *Achatina fulica*: Bobkova *et al.* 2004b) and aquatic pulmonates (e.g., the snail *Lymnaea stagnalis*: Stoll 1973, Bobkova 1998, the slug *Onchidium verruculatum* (Cuvier, 1830): Katagiri and Katagiri 1998, the freshwater limpets *Ancylus fluviatilis* and *Latia neritoides*: Meyer-Rochow and Bobkova 2001) have revealed that the corneae are structurally similar to each other (Fig. 3A-B). We believe that the difference in thicknesses reflects the degree to which protection of the eye, for example in terrestrial snails against desiccation, is at a premium.

The cornea is composed of a monolayer of elongated, flattened, and *in vivo* transparent cells, reaching from the basal lamina to the optical cavity. The cells in aquatic species are strongly interdigitating. The inner surface of the corneal cells forms short irregular microvilli that are oriented toward the lens. The nuclei are situated in the basal cytoplasm. The flaky but electron-translucent cytoplasm of the corneal cells contains a few mitochondria, glycogen particles, rough endoplasmic reticulum, free ribosomes, and, directed toward the vitreous body, secretory vesicles filled with electron-dense granular material (Fig. 3A-B). The corneal cells are laterally connected with each other and with the most anterior retinal cells at the end of the cornea by septate junctions and *zonulae adhaerentes*. Basally they are anchored to the basal lamina by hemi-desmosomes. Corneal cells, together with retinal supportive cells, are known to contain secretory vesicles. The electron-dense granular content of the vesicles closely resembles that of the vitreous body and the lens.

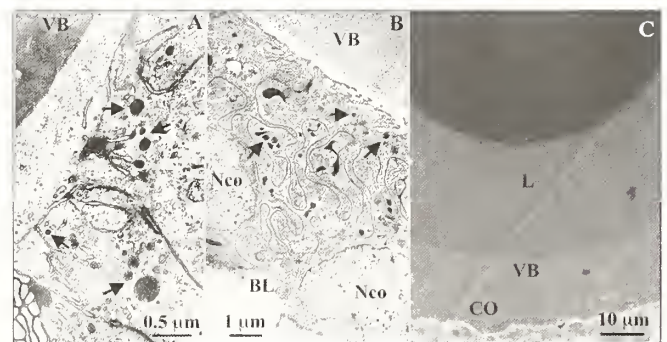


Figure 3. Electron micrographs of approximately longitudinal sections through the cornea: (A) *Deroceras agreste*, (B) *Radix peregra* and section through lens and cornea in (C) *Lymnaea stagnalis*. CO, cornea; L, lens; Nco, nucleus of corneal cell; VB, vitreous body; Arrows, secretory vesicles.

Therefore, the corneal cells are thought to be involved in the genesis of lens material (e.g., in *Cornu aspersum aspersum*: Eakin and Brandenburger 1967a; *Limax flavus*: Kataoka 1977; *Lymnaea stagnalis*: Stoll 1973, Bobkova 1998; *Arion rufus* (Linnaeus, 1758); and *Deroceras agreste*: Zieger *et al.* 2008). Blumer (1995) described the transport of electron-dense material toward the lumen in juvenile marine non-pulmonate gastropods.

In an aquatic environment the cornea is not very useful as a refracting interface, and any necessary refraction therefore depends on the properties of the lens alone. Obviously, we have to be mindful of the fact that the cornea, if in air, shortens the focal length of the optical system, but even so, it has earlier been shown that in the terrestrial snails *Cepaea nemoralis* and *Trichia hispida* only the lenses play a significant role as the refractory surfaces (Gál *et al.* 2004). We therefore assume that the lens is the main element of the optical system not just in the aquatic, but in terrestrial species as well.

Lens

Gastropod eyes possess an "acellular" lens (Eakin 1972) and a vitreous body that shares certain features with the lens. Freshwater snails like *Lymnaea stagnalis*, *Radix peregra*, *Physa fontinalis*, and limpets like *Ancylus fluviatilis* and *Latia neritoides* have spherical lenses. However, all of the studied terrestrial snails and slugs (Newell and Newell 1968, Brandenburger 1975, Eakin *et al.* 1980, Meyer-Rochow and Bobkova 2001, Bobkova *et al.* 2004a, Zieger *et al.* 2008) as well as the marine slug *Onchidium verruculatum* (Katagiri and Katagiri 1998) have ovoid lenses of lamellar substructure with optical axes either along or across their ovoid outlines. Spherical lenses of the aquatic species are usually hard enough to permit their surgical removal from the eye for further study. The ovoid lenses of the terrestrial snails and slugs are also hard (Bobkova *et al.* 2004a), but some stylommatophoran snails, like *Strophochelins* sp. (Pfeiffer, 1842), possess a jelly-like lens that tears easily during dissection (Oswaldo-Cruz and Bernardes 1982).

The spherical lenses of most aquatic and terrestrial species can easily be isolated from the retinal cavity, but it is practically impossible to separate the non-spherical lenses (Zhukov *et al.* 2002) from the vitreous body of the freshwater pulmonate snail *Planorbis cornutus* (Bobkova *et al.* 2004a), suggesting intimate connections and possibly a common origin of lens and vitreous body.

To keep the size of the eye sufficiently small, the focal length needs to be kept short in relation to the size of the lens. This requires the lens to be more or less spherical. However, a homogeneous and spherical lens would suffer from serious spherical aberrations, in which rays off axis are refracted too severely, so that a sharp image cannot be ob-

tained and an undesirably large blurred circle is created instead. Another problem is that the lens would have rather a long focal length (Land and Nilsson 2002).

Matthiessen (1886) showed that both these problems could be overcome if the lenses were optically inhomogeneous with a gradient of higher to lower refractive index from center to periphery. Then, rays entering the lens could be bent continuously within the lens through refraction and not just at the lens's outer and inner surfaces. A lens design like this would effectively increase the power of the lens and shorten its focal length, correct spherical aberration, and, thus, reduce or even abolish the deleterious effects of an optically homogeneous lens (Land 1984).

As a rule, unstained transverse sections through a snail's lens sometimes reveal regular concentric layers that are discernible under both light and electron microscopes (e.g., the marine slug *Onchidium verruculatum*: Katagiri and Katagiri 1998; freshwater and terrestrial snails and slugs: Bobkova *et al.* 2004a, Zieger *et al.* 2008; and freshwater limpets: Meyer-Rochow and Bobkova 2001) (Fig. 3C). A heterogeneous staining pattern can furthermore indicate an optically inhomogeneous construction of the lens (Hamilton *et al.* 1983, Bobkova *et al.* 2004a).

Demian and Yousif (1975) demonstrated that the lens, laid down in the lumen of the eye, grows through the addition of concentric layers of secretions from the centre outwards. Thus, it seems that lenses with a radial gradient of refractive index should be relatively easy to build because proteins varying in optical density may be synthesized and laid down successively. However, the chemical composition of the acellular gastropod lenses remains enigmatic. The sea hare *Aplysia californica* (Cooper, 1863) is the only gastropod that has been examined for crystallins, i.e., proteins known to be responsible for the optical properties of transparent lenses and corneae (Tomarev and Piatigorsky 1996).

Vitreous body

In order to have a potential for image formation, the lens and the retina need to be separated (Land 1981, Seyer 1994, Seyer *et al.* 1998, Gál *et al.* 2004). In the camera-type eyes, separation of the lens and retina is achieved by presence of a vitreous body. The vitreous body surrounds the lens and has contact with the receptive and non-receptive parts of the retina. The vitreous body and lens both contain grainy or tubular substructures, but those making up the vitreous body are always less electron-dense than those of the lens interior (Fig. 3C). The vitreous body is considerably less extensive in many terrestrial pulmonates, and larger in some freshwater pulmonates that demonstrate good visual abilities. The near lack of separation between the lens and the retina in most terrestrial pulmonates seems to indicate that their eyes are not built to receive a focused image.

The vitreous humor is continuous between the additional and the main retinae in *Agriolimax reticulatus* (Newell and Newell 1968) and in *Deroceras agreste* (Zieger *et al.* 2008).

ULTRASTRUCTURE OF THE RETINAL CELLS

Photoreceptors

With rare exceptions, *e.g.*, *Planorbarius corneus* (Zhukov *et al.* 2002), the majority of the species investigated have two morphologically distinct kinds of “rhabdomeric photoreceptors” (Eakin 1963). The first kind (“type I photoreceptors”) is characterized by long microvilli and massive aggregations of so-called “photoc vesicles” (Eakin 1990). The second photoreceptor type (“type II”) is less common. It lacks the dense packing of photoc vesicles and bears shorter microvilli. The type II photoreceptor has been described from the retinae of the terrestrial snails *Cornu aspersum aspersum* (Brandenburger 1975), *Succinea putris* (Linnaeus, 1758) (Zunke 1979), *Strophochelius* sp. (Oswaldo-Cruz and Bernardes 1982), *Trichia hispida* (Bobkova *et al.* 2004a), the terrestrial slugs *Limax maximus*, *Ariolimax californicus* (Cooper, 1872) (Eakin and Brandenburger 1975b), *Athoracophorus bitentaculatus* (Quoy and Gaimard, 1832) (Eakin *et al.* 1980), *Limax flavus* (Kataoka 1975), and *Deroceras agreste* (Zieger *et al.* 2008). The marine slugs *Onchidium verruculatum* (Katagiri *et al.* 1995), and the freshwater basommatophoran snails *Lymnaea stagnalis* (Stoll 1973, Bobkova 1998), *Radix peregra*, and *Physa fontinalis* (Bobkova *et al.* 2004a) have the second photoreceptor type as well.

Photoreceptor cells with long microvilli may have a finger-like (as in freshwater species (Bobkova *et al.* 2004a) and the slug *Deroceras agreste* (Zieger *et al.* 2008)) (Fig. 4A-C), flared (as in *Arion rufus* (Zieger *et al.* 2008)) (Fig. 5) or short and dome-shaped apical portion as in *Ariolimax californicus* (Eakin and Brandenburger 1975b) and *Cepaea nemoralis* (Bobkova *et al.* 2004a). The short microvilli of the photoreceptors may be brush-like, whorled (as in the distal depression of the retina), or regularly arranged (Fig. 4D-E). Electrophysiological results suggest in *Limax flavus* that type I photoreceptors operate in dim and type II photoreceptors in bright light (Suzuki *et al.* 1979). However, we cannot exclude the possibility that the cells belong to the same functional type of photoreceptor and represent stages in the process of receptor cell renewal (death and replacement) in the mature retina. Moreover, based on electrophysiological recordings from a variety of gastropods (*e.g.*, Dennis 1967, Gillary and Wolbarsht 1967, Hughes 1970, Gillary 1974, Berg 1978, Suzuki *et al.* 1979, Zhukov and Gribakin 1990, Chernorizov *et al.* 1994), there is no convincing evidence for more than a single spectral sensitivity peak between 480 and 505 nm wavelength, suggesting that at least physiologically there is only one type of receptor.

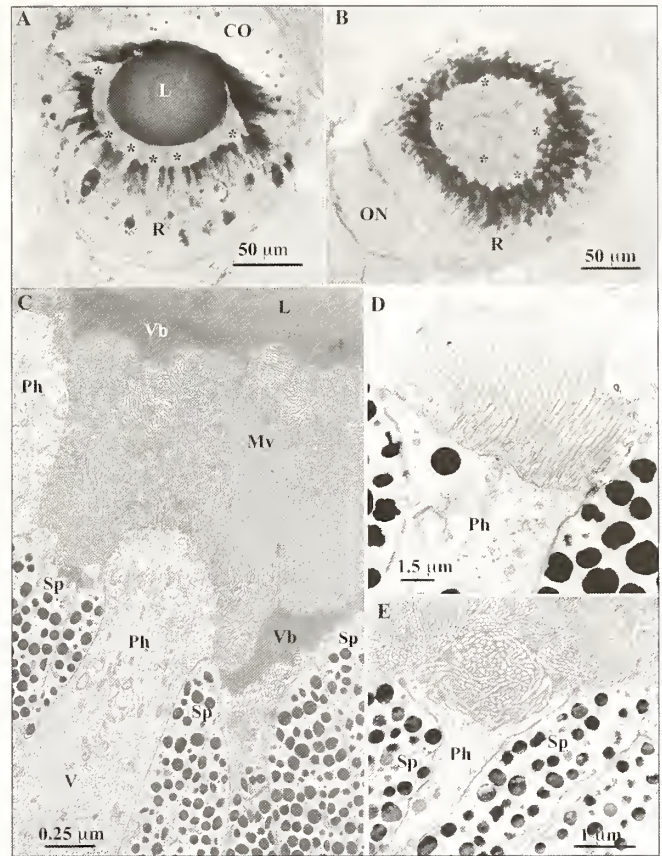


Figure 4. Light (A and B) and electron (C, D, and E) micrographs, featuring two morphological types of photoreceptor cells in pulmonates. Nearly longitudinal (A and C) and transverse (B) sections through the eye of *Deroceras agreste*, showing finger-like apices (asterisks). Photoreceptors with short and regularly arranged microvilli in *Lymnaea stagnalis* (D) and whorled microvilli in the distal depressions of the *Trichia hispida* retina (E) are discernible. CO, cornea; L, lens; Mv, light sensitive layer of microvilli; ON, optic nerve; Ph, photoreceptor cells; R, retinal cup; Sp, supportive (pigmented) cells; Vb, vitreous body. A, B, and C from Zieger *et al.* 2008; D and E from Bobkova *et al.* 2004a with permission of John Wiley and Sons, Inc.

As evident from *in vivo* observations and sections of fixed tissues, the retinae of all pulmonate snails are deeply pigmented. However, in spite of the presence of specialized supportive (or pigmented) cells, photoreceptor cells also contain screening pigment granules in freshwater snails (Bobkova 1998, Bobkova *et al.* 2004a) and limpets (Meyer-Rochow and Bobkova 2001) as well as in the terrestrial snails *Trichia hispida* (Bobkova *et al.* 2004a) and *Cornu aspersum aspersum* (Eakin and Brandenburger 1982) and the marine slug *Onchidium verruculatum* (Katagiri *et al.* 1995) (Fig. 6A-B). Photoreceptors in terrestrial slugs (Newell and Newell 1968, Eakin and Brandenburger 1975b, Kataoka 1975) and

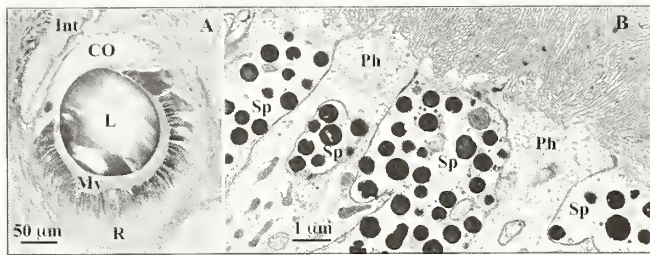


Figure 5. Light (A) and electron (B) micrographs of longitudinal sections through eye and apical portion of the retina of *Arion rufus* showing shallow retina (A) and flared apices of photoreceptor cells with long microvilli (B). CO, cornea; Int, integument; L, lens; Mv, microvillar layer; Ph, photoreceptor cells; Sp, pigmented supportive cells. A and B from Zieger *et al.* 2008 with permission of John Wiley and Sons, Inc.

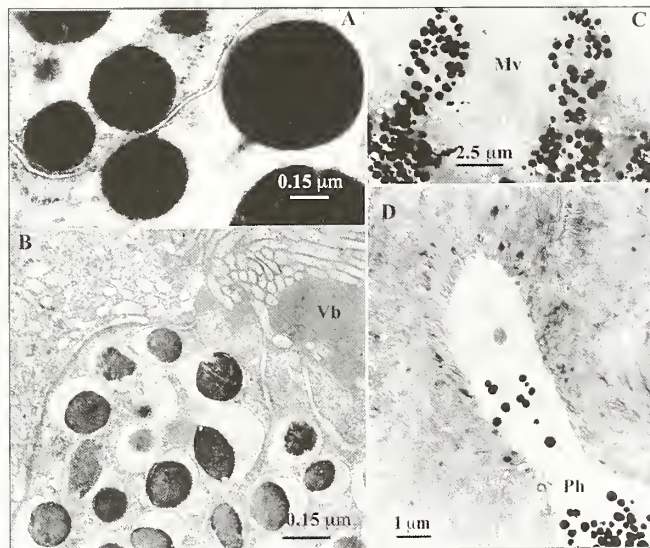


Figure 6. Electron micrographs, showing pigment granules in the supportive cells of *Arion rufus* (A) and pigmented granules, affected by bright light, in the photoreceptor cell of *Deroceras agreste* (B), with pigment granules filling the apices of the photoreceptor cells following deep light adaptation (C) and fewer pigment granules following deep dark adaptation (D) in the photoreceptor cells of *Lymnaea stagnalis*. Mv, microvilli; Ph, apex of photoreceptor cell; Vb, vitreous body. C and D from Bobkova *et al.* 2004a with permission of John Wiley and Sons, Inc.

the snail *Cepaea nemoralis* (Bobkova *et al.* 2004a) contain no screening pigment granules. A certain vertical light-dependent pigment granule displacement (often called “migration”) was revealed in freshwater snails (Bobkova 1998, Zhukov *et al.* 2002, Bobkova *et al.* 2004a). In samples prepared for morphological investigations during periods of total light adaptation, we were able to observe that the fin-

ger-like apices became filled in with screening pigment granules. Conversely, pigment granule dispersion occurred when a light-adapted eye was exposed to darkness and, thus, indicates dark adaptation (Bobkova 1998) (Fig. 6C-D).

Our ultrastructural observations have shown that photoreceptor cell types I and II occur in close approximation to each other and are jointly present at the level of the retinal pigment layer in the eye of, for example, *Lymnaea stagnalis* (Bobkova 1998) and *Cepaea nemoralis* (Bobkova *et al.* 2004a). However, we never found any specialized mechanical or functional contacts between the two types of these cells.

Microvilli and photic vesicles

One of the most important selective pressures in the evolution of photoreceptors appears to have been the need to increase the area available for visual membranes—in other words, to lay the foundation for an increase in photosensitivity that depended on the maximization of space for photoreceptive membranes. Rhabdomeric photoreceptors achieve this by increasing the total number of microvilli. The small diameter of an individual microvillus, which is approx. 600 Å in the dark-adapted eye irrespective of the type of photoreceptor, helps in this regard but also poses a lower limit for miniaturization as the organization and dimensional characteristics of the microvilli appear to be similar in all of the invertebrate eyes investigated to date.

An axial cytoskeleton is present in the tubular lumen of the microvilli; it is formed by bundles of fibrils that run along the length of the microvilli and are connected to the membrane (Fig. 7A). Microvilli reach their highest degree of order during periods of dark adaptation but are found to enlarge (“swell up”), following brief exposures to bright light, or to become dramatically disorganized when an isolated eye is exposed to bright light for a longer period of time (Bobkova 1998) (Fig. 7B). The processes of microvillar disruptions by light in the snail eye are likely to be similar to the changes that bright light exposure causes in the compound eyes of crustaceans (reviewed by Meyer-Rochow 1994, 2001) and insects (Meyer-Rochow *et al.* 2002), where bright light is known to affect the axial cytoskeleton and the lipid fraction of the microvillar membrane itself (Kashiwagi *et al.* 1997, 2000).

Photic vesicles are important and characteristic cytoplasmic organelles in the eyes of gastropod molluscs (Fig. 7C). Whittle (1976) discussed the controversial origin of the photic vesicles, *i.e.*, of Golgi apparatus origin according to Eakin and Brandenburger (1967b) but vesiculations of the smooth endoplasmic reticulum according to Kataoka (1975), and concluded that the evidence is entirely consistent with reticular specializations. Eakin (1990) has summarized data on structure, origin, fate, and function of the

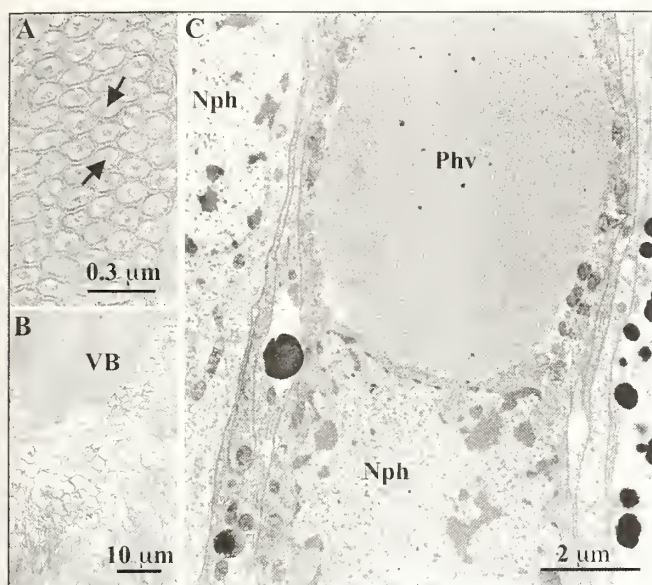


Figure 7. Electron micrographs, showing transverse section through microvilli (A) and microvillar layer affected by bright light in the eye of *Lymnaea stagnalis* (B) and aggregation of photic vesicles (C) in the perinuclear area of photoreceptor cells in *Cepaea nemoralis*. Arrows, axial cytoskeleton; Nph, nuclei of photoreceptor cells; Phv, photic vesicles; VB, vitreous body.

photic vesicles as “transporters of a photopigment retinochrome and calcium” and likened them to the lamellated bodies in cephalopod photoreceptors shown by Hara *et al.* (1967) to contain retinochrome. Later, fluorescent histochemical techniques, using a reducing agent, have shown that rhodopsin and retinochrome are present in the microvillar and somatic layers of the stalks of the eyes of the marine pulmonate slug *Onchidium verruculatum* (Katagiri *et al.* 2002) and the terrestrial slug *Limax flavus* (Ozaki *et al.* 1983).

Using antibodies against squid retinal proteins, Katagiri *et al.* (2001) determined the localization of three retinal proteins (rhodopsin, retinochrome, and retinal-binding protein), and thus demonstrated the presence of a rhodopsin-retinochrome system in the eyestalk of the marine pulmonate *Onchidium* sp. Later, Katagiri *et al.* (2002) confirmed by fluorescence histochemistry the presence of rhodopsin and retinochrome in specific regions of the retina. Accordingly, the visual pigment rhodopsin is present in the microvilli of the photoreceptive cells, while the photic vesicles themselves may be regarded as a store for retinaldehyde in the form of retinochrome-chromophore.

Rhodopsin and retinochrome function cooperate to mutually regenerate photopigment (Terakita *et al.* 1989). Upon illumination, rhodopsin is converted to metarhodopsin, and retinochrome to meta-retinochrome. The 11-cis-

retinal in rhodopsin is photoisomerized to the all-trans configuration. Conversely, the all-trans-retinal in the retinochrome is photoisomerized to its 11-cis-isomer. The 11-cis-retinal is required for rhodopsin formation. In the dark, rhodopsin and retinochrome are regenerated from these two isomers by chromophore exchange.

Supportive pigmented cells

Supportive pigmented cells are located between the photoreceptor cells. Their apical portion bears very short membranous microvilli-like projections into the vitreous body. The cells form the border of the fixed pupil aperture. In freshwater snails, limpets, and some terrestrial species, supportive pigmented cells have column-like apices (e.g., *Lymnaea stagnalis*: Stoll 1973, Zunke 1979; *Onchidium verruculatum*: Katagiri *et al.* 1995, Bobkova 1998; *Latia neritoides* and *Ancilus fluviatilis*: Meyer-Rochow and Bobkova 2001; *Planorbarius cornuus*: Zhukov *et al.* 2002; *Radix peregra*, *Physa fontinalis*: Bobkova *et al.* 2004a). However, in some terrestrial slugs and snails, the supportive pigmented cells envelope the photoreceptors, send deep and multiple projections into the photoreceptor cytoplasm, and are crowded with innumerable pigment granules (viz., *Helix pomatia*: Schwalbach *et al.* 1963, Röhlich and Török 1963; *Cornu aspersum aspersum*: Eakin and Brandenburger 1967a; *Limax flavus*: Kataoka 1975; *Ariolimax californicus*: Eakin and Brandenburger 1975b; *Achatina fulica*: Tamamaki and Kawai 1983; *Cepaea nemoralis*: Bobkova *et al.* 2004a; *Dero-ceras agreste* and *Arion rufus*: Zieger *et al.* 2008). However, in species with finger-like apices (cf., section on “Photoreceptors”) they never penetrate into the spaces between the latter. In the nocturnal slug *Limax maximus*, lateral branches along the sides of the photoreceptor cells have been described to often lack pigment granules (Eakin and Brandenburger 1975b).

The nuclei of the supportive (pigmented) cells are located in the basal region of the somatic and plexiform layers. They are much smaller than the nuclei of the photoreceptor cells and are identifiable by their condensed heterochromatin (Fig. 8A). Multiple rings of rough endoplasmic reticulum together with large numbers of mitochondria are present in the perinuclear area, suggesting that the supportive pigmented cells are synthetically active retinal cells. The cells themselves are anchored by hemi-desmosomes to the basal lamina.

Although the chemical nature of the retinal screening pigment has not been analyzed in detail, generally it is assumed that the pigment is a form of the melanin (e.g., *Lymnaea stagnalis*: Land 1968, Stoll 1973, Bobkova 1996, and *Cornu aspersum aspersum*: Eakin and Brandenburger 1967a, 1967b).

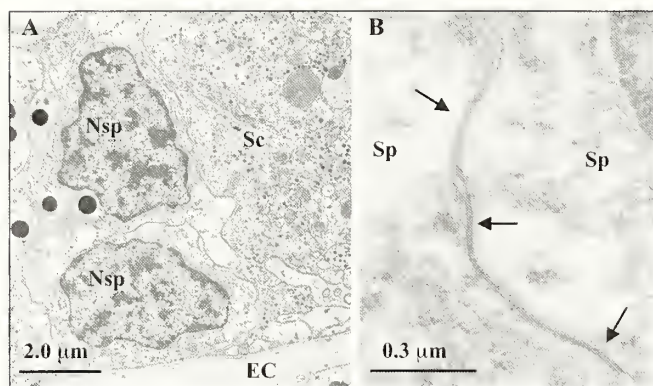


Figure 8. Electron micrographs, showing (A) nuclei of pigmented supportive cells (Nsp) and sites in (B) of gap junctions (arrows) between adjacent pigmented supportive cells (Sp) in *Arion rufus*. EC, eye capsule; Sc, neurosecretory cell. From Zieger *et al.* 2008 with permission of John Wiley and Sons, Inc.

Cellular contacts between adjacent cells

As a rule, and not restricted to molluscs, adjacent cells are connected with each other by mechanical cellular contact specializations like *zonulae adherentes*, located apically just above the septate junctions. The latter resemble those examined in the leech photoreceptors by Aschenbrenner and Waltz (1998) and are thought to contribute to the maintenance of the cell polarity. Contacts of this nature are seen in the retinæ of *Ariolimax californicus* (Eakin and Brandenburger 1975b), *Limax flavus* (Kataoka 1975), *Athoracophorus bitentaculatus* (Eakin *et al.* 1980), and *Lymnaea stagnalis* (Bobkova 1998). The existence of finger-like folds, projecting into adjacent cells, has been reported from the eyes of *Lymnaea stagnalis* by Bobkova (1998) and *Ariolimax californicus* by Eakin and Brandenburger (1975b). Similar cytoplasmic folding is known from vertebrate epithelial cells (*i.e.*, bronchial and intestinal kinds) to enable these cells to change their length. A property such as this, if it held true for the unusual mechanical contacts with folds, would agree with observations made by Stoll (1973) on light-dependent retinomotoric cell extensions and contractions in the retina of *Lymnaea stagnalis*.

The supportive cells (with heavily pigmented extensions, but only near their distal ends) form multiple gap-junctions between each other in *Lymnaea stagnalis* (Bobkova 1998) and *Arion rufus* (Zieger *et al.* 2008) (Fig. 8B). It appears as if this type of cell has a kind of syncytium-like intraretinal net.

Neurosecretory cells

The retinal cells that we termed 'neurosecretory' in *Arion rufus* (Zieger *et al.* 2008) are likely to belong to cells

that are known in *Limax flavus* as "large ganglionic cells of the nervous system" (Kataoka 1975) and in *Corneum aspersum aspersum* (Brandenburger 1975), *Ariolimax reticulatus* (Newell and Newell 1968), and *Lymnaea stagnalis* (Stoll 1973, Bobkova 1998) as ganglion cells.

The cell types listed above are similar in appearance, contain a very large nucleus, and are endowed with prominent rough endoplasmic reticulum, numerous granulated osmiophilic dense-core and clear vesicles, and large liposomes or pigment-granule-like bodies, similar to the lipochondria of the *Aplysia* sp. ganglion cells described by Baur *et al.* (1977). Following Strumwasser *et al.* (1979), we have accepted the term "neurosecretory cells" for the cells in question in *Arion rufus*.

These large oval cells were found to form a single cluster in a delimited region of the eye of *Arion rufus* (Zieger *et al.* 2008) (Fig. 9A-C), and in *Trichia hispida* and *Cepaea nemoralis* (Zieger, unpubl. data). In the freshwater snails *Lymnaea stagnalis* (Bobkova 1998), *Radix peregra*, and *Physa fontinalis* (Zieger, unpubl. data), retinal cells of this type are diffusely distributed among other retinal cells. No synaptic contacts were found on the surface of the cell body of these cells in *A. rufus* (Zieger *et al.* 2008) and *Lymnaea stagnalis* (Bobkova 1998). However, Brandenburger (1975) demon-

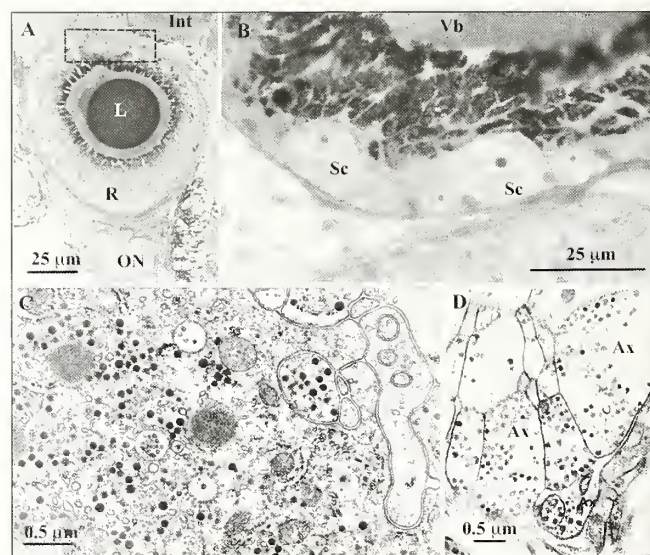


Figure 9. Light micrographs of tangential section (A) through cluster of neurosecretory cells (framed) and (B) enlargement of the cluster in the eye of *Arion rufus*. Electron micrographs of perinuclear region (C) and axons (D) containing dense-core vesicles in *Arion rufus*. Ax, axons; Int, integument; L, lens; R, retina; Sc, secretory cells; Vb, vitreous body. A and B from Zieger *et al.* 2008 with permission of John Wiley and Sons, Inc.

strated synaptic-like structures on the surface of the “ganglion” cells in *Cornu aspersum aspersum*.

The axons of the neurosecretory cells can be identified in the plexiform layer of the retina by their contents of dense core vesicles (Fig. 9D). We cannot completely rule out the possibility that the neurosecretory cells in the eye of *Arion rufus* are a kind of neuroendocrine cell type that releases its vesicular content directly into the body fluid to reach more distant effector organs.

As to the function of the retinal neurosecretory cells, we can only speculate that they could be involved in various aspects of the reproductive cycle (*i.e.*, gonadal development, sexual maturation, egg laying) or in some aspect of metabolic regulation. It was earlier shown that the retinal neurons in the marine non-pulmonate gastropods *Bulla gouldiana* (Pilsbry, 1895) and *Aplysia californica* are capable of generating a circadian periodicity. Actually, the cells are competent circadian retinal pacemakers and as in circadian pacemakers, the oscillators entrain to cycles of light and darkness, especially the 24-h light/dark cycle of the environment (*cf.*, review by Whitmore and Block 1996).

In behavioural experiments with *Arion rufus*, it was shown that these slugs have a circadian rhythm (Lewis 1969). In fact, that light is highly effective in entraining circadian rhythmicity is also known for other gastropods like slugs (*Limax flavus*: Segal 1960; *Agriolimax reticulatus*: Newell and Newell 1968), terrestrial snails like *Helix pomatia* (Jeppesen 1977), *Cornu aspersum aspersum* (Bailey 1981), *Helix lucorum lucorum* (Linnaeus, 1758) (Flari and Lasariadou-Dimitriadou 1995), and *Achatina achatina* (Hodasi 1982) as well as the slugs *Limax pseudoflavus* (Evans, 1978) (Ford and Cook 1988, 1994), *Deroceras reticulatum* (Müller, 1774), and *Arion distinctus* (Mabille, 1868) (Hommary *et al.* 1998). However, the possession of an internal oscillator, which is capable of measuring the photoperiod has not been demonstrated in these pulmonate species. The notion that it is the retinal neurons, which express circadian rhythmicity themselves, has yet to be proven.

OPTICAL CALCULATIONS

In 1984 Hamilton and Winter pointed out that the degree of accuracy of the behavioral data on visual abilities can be checked by carrying out a resolution estimate based on the optical and structural characteristics of the eye. In other words, in order to know a snail eye's functional limitations, it is imperative to possess some information on the eye's optics and structural organization. Resolving power and sensitivity are key parameters in this context, and both can be approximated from anatomical and optical data. To determine the limitations of the optical system of the eyes in pulmonates, we followed methods (with some modifications: *cf.*, Bobkova *et al.* 2004a, Gál *et al.* 2004) that were used earlier with considerable success in comparisons of eyes in some caenogastropods (Seyer 1992, 1994, Seyer *et al.* 1998). The methods described by Nilsson *et al.* (1988) and by Seyer (1992) were used to determine the focal lengths of freshly isolated lenses. The same methodological approach allowed us to compare optical systems in different pulmonate gastropods (Tables 1-3).

All of the pulmonate gastropod eyes investigated to date operate with fixed focal-length optics, which means that at least the principal focal length cannot be changed. The fixed focal-length optics design is described in some vertebrates (Walls 1942), who in order to accommodate to different distances adjust the position of the lens relative to the retina. However, in the absence of accommodation mechanisms in the eyes of gastropods, it appears that the almost infinite depth of focus characteristic of the eyes of aquatic gastropods makes accommodation unnecessary (Land 1981).

The shape of the gastropod eye lens was found to be spherical in aquatic species and elliptic, with an optical axis either across or along the lenticular ellipse, in terrestrial species. There are, however, exceptions: the lens of the aquatic snail *Planorbis cornutus* is rather more elliptic than spherical (Zhukov *et al.* 2002) and the terrestrial slug *Deroceras agreste* has a spherical lens (Zieger *et al.* 2008). The

Table 1. Comparative eye parameters of terrestrial pulmonates based on light and electron microscopy (in μm). Values are means.

	<i>Arion rufus</i>	<i>Deroceras agreste</i>	<i>Cepaea nemoralis</i>	<i>Trichia hispida</i>	<i>Agriolimax reticulatus</i>
Size of eyeball	240 × 290	220 × 220	312 × 320	142 × 220	140 × 180
Size of lens	150 × 200	110 × 110	152	81	130
Diameter of aperture	100	80	107	92	—
Center-to-center separation of receptors	5.6	17.0	21.0	15.0	6.0
*Receptor length	13.8	27.8	3.4-20.0	3.0-15.0	25.0-30.0
Authors	Zieger <i>et al.</i> (2008)		Bobkova <i>et al.</i> (2004)		Newell and Newell (1968)

* Values based on thickness of microvillar layer.

Table 2. Comparative eye parameters of aquatic pulmonates based on light and electron microscopy (in μm). Values are means.

	<i>Ancylus fluviatilis</i>	<i>Latia neritoides</i>	<i>Lymnaea stagnalis</i>	<i>Radix peregra</i>	<i>Physa fontinalis</i>	<i>Planorbarius corneus</i>
Size of eyeball	100 × 100	150 × 175	210 × 270	160 × 200	150 × 170	240 × 275
Size of lens	60	90	120	94	80	136
Diameter of aperture	43	63	60	73	65	140
Center-to-center separation of receptors	2.5	6.5	8.3	4.5	8.9	6.2
*Receptor length	7.0	31.0	71.0	18.0	49.1	18.5
Authors	Meyer-Rochow and Bobkova (2001)		Bobkova <i>et al.</i> (2004a)			

* Values based on thickness of microvillar layer.

Table 3. Comparative mathematically determined optical parameters in different species of pulmonate gastropods. Values are means; the symbol '—' denotes missing values.

Species	Principal focal length of the lens (μm)	Relative aperture	Matthiessen's ratio	Angular receptor spacing (degrees)	F- number	Diameter of Airy-disc (μm)	Resolving power (radian^{-1})	Sensitivity ($\mu\text{m}^2\text{sr}^{-1}$)	Authors
<i>Arion rufus</i>	848	0.10	—	0.40	—	—	—	—	Zieger <i>et al.</i> (2008)
<i>Deroceras agreste</i>	207	0.40	3.7	4.70	2.5	3.00	—	—	Zieger <i>et al.</i> (2008)
<i>Cepaea nemoralis</i>	149	0.70	—	8.00	1.3	1.60	4.0	8.00	Gál <i>et al.</i> (2004)
<i>Trichia hispida</i>	122	0.80	—	13.00	1.2	1.50	2.5	4.00	Gál <i>et al.</i> (2004)
<i>Agriolimax reticulatus</i>	100	—	2.8	15.00	—	—	—	—	Newell and Newell (1968)
<i>Lymnaea stagnalis</i>	174	0.30	2.9	2.70-5.20	2.9	3.60	6.3-12.0	0.04-1.80	Gál <i>et al.</i> (2004)
<i>Radix peregra</i>	128	0.60	2.7	2.0-6.50	1.7	2.00	0.2-16.5	0.02-0.20	Gál <i>et al.</i> (2004)
<i>Physa fontinalis</i>	116	0.60	2.9	4.00-5.00	1.8	2.20	7.0-8.0	0.20	Gál <i>et al.</i> (2004)
<i>Planorbarius corneus</i>	241	0.60	3.5	2.50	1.8	2.00	13.0	1.40	Gál <i>et al.</i> (2004)

lenses in all species studied presumably possess a radial gradient of refractive index (*i.e.*, are optically in-homogeneous) irrespective of lens shape.

It is generally assumed that terrestrial animals cannot exploit the advantages of a spherical graded index lens. Instead, by having a curved outer surface on the cornea, they must make use of the low refractive index of air (1.0). Because the cornea then provides much of the refracting power, an interior lens can be designed specifically, for example, to correct spherical aberration (Land 1984, Nilsson 1989).

However, on the basis of our calculations it appears that the integument-cornea lens complex in the terrestrial snails *Cepaea nemoralis* and *Trichia hispida* is optically much less important than the refractive power of the lens alone (Gál *et al.* 2004). A similar assessment, not based on any calculations, was made for the slugs *Arion rufus* and *Deroceras agreste* (Zieger *et al.* 2008). For accuracy, we have made the

essential calculations, and have included the mean values obtained into this review (see below).

The focal length of the system of two lenses (f_s) can be calculated as:

$$1/f_s = 1/f_L + 1/f_C - x/f_L f_C,$$

where f_L is principal focal length of the lens, f_C is focal length of the integument-cornea complex and x is the distance between the two lenses centers.

The focal length of the integument-cornea complex can be calculated as described by Gál *et al.* (2004).

Thus, in *Cepaea nemoralis* the focal length of the lens alone is 149 μm , and the focal length of the system composed of the two lenses (integument-cornea plus lens) is 144 μm . The corresponding figures are 122 and 113 μm for *Trichia hispida*, 207 and 170 μm for *Deroceras agreste*, and 848 and 450 μm in *Arion rufus*. As is obvious, in the eyes of the snails *C. nemoralis* and *T. hispida*, the shortening is only

5 to 9 μm , but in the eyes of the slugs it is *ca.* 400 (*A. rufus*) and 40 μm (*D. agreste*).

As we see here, the contribution of the first lens, the integument-cornea complex in the snails' eyes, is surprisingly small and in slugs, the refractive power of the integument-cornea complex looks very significant. However, at this point of our discussion, we still continue to argue that the lens, but not the integument-cornea, is the principal optical element of the eyes in terrestrial gastropods, just as in aquatic species. It is very likely that the optical properties of the lens in the terrestrial gastropods reflect the lens properties that their marine ancestors might have had.

The quality of the images produced by the isolated lenses of both terrestrial and aquatic gastropods demonstrates that the latter are corrected for spherical aberration (Gál *et al.* 2004). Therefore, we may conclude that lenses in both aquatic and terrestrial pulmonates, presumably possess a radial gradient of refractive index (*i.e.*, are optically inhomogeneous), irrespective of lens shape. However, to entirely eliminate spherical aberration it is not enough to have refractive-index gradients. The lens should be spherically symmetrical and have a ratio of focal length to lens radius of about 2.5 (Warrant and McIntyre 1993). Newell and Newell (1968) have shown that the lens in the terrestrial slug *Agriolimax reticulatus* has a focal length of 2.8 radii and, on that basis, concluded that the lens must have a graded refractive index.

The ideal spherical geometry, combined with a gradient of refractive index and an F-number of 2.9, endows *Lymnaea stagnalis* with a perfect aplanatic lens and superb optical image quality. Other species, like *Radix peregra*, *Physa fontinalis*, and *Planorbarius corneus* come close to the optimum, but imperfections in the optics such as low F-numbers (1.7, 1.8, 1.8, and 1.9, respectively) (Table 3) of the eyes manifest themselves as degradations in the quality of the image formed on the retina. Spherical aberration must be worse in the eyes of the terrestrial snails *Cepaea nemoralis* and *Trichia hispida* because of large, in relation to their focal length, apertures (0.7 and 0.8 compared to 0.3 in *L. stagnalis*) and low F-numbers (1.3 in *C. nemoralis* and 1.2 in *T. hispida*) as their eyes are designed to capture as much light as possible (Table 3) (Gál *et al.* 2004). The slug *Deroceras agreste* was found to have a high F-number equaling 2.5 and a spherical lens very likely free of aberration (Zieger *et al.* 2008).

Another source of lens imperfection, namely chromatic aberration, arises because the transparent material of the lens is invariably dispersive, that is, light of shorter wavelength is refracted by the material more strongly than light of longer wavelengths (Warrant and McIntyre 1993). However, chromatic aberration becomes important only when the diameter of the aperture exceeds about 500 μm (Land 1981). We therefore did not take chromatic aberration into con-

sideration because the species studied have apertures in the range of 40 μm (*Ancylus fluviatilis*) (Meyer-Rochow and Bobkova 2001) to 140 μm (*Planorbarius corneus*) (Zhukov *et al.* 2002).

Even if the effects of spherical and chromatic aberration are negligible, the image produced by the eye can still be blurred. This limitation in image quality is referred to as diffraction.

In general, at any given wavelength, lenses with larger apertures will have narrower Airy discs (the central peak of a diffraction blur-circle), and thus suffer least from diffraction. For instance, aperture and Airy disc are 60 μm and 3.6 μm in *Lymnaea stagnalis*, 80 and 3.0 μm in *Deroceras agreste*, 92 and 1.5 μm in *Trichia hispida*, 107 and 1.6 μm in *Cepaea nemoralis*, and 140 and 2.0 μm in *Planorbarius corneus* (Tables 1 and 3). Larger apertures lead to losses in image quality due to aberration, and therefore for each eye design there must be some sort of compromise between diffraction and aberration.

Do the gastropods make use of their definitely advanced optical designs? It appears that even if eye optics can focus aberration free and diffraction-limited images, there are still anatomical limitations within the eye, which can destroy the potential for high resolving power of the gastropod eye.

Retinal geometry

If the position of the retina does not coincide with the sharp image plane (= position of the focal point within the microvillar layer), it would lead to wide receptive fields in individual receptors and thus result in considerable decreases of resolution. Such severely under-focused eyes occur in the terrestrial snails *Cepaea nemoralis* and *Trichia hispida*, where the sharp image falls just below the light-receiving microvilli within the retina (Gál *et al.* 2004). The under-focusing leads to a blurred image and loss of fine visual detail that the optics of these snails is able to provide.

The situation is even worse in the slugs *Arion rufus* and *Deroceras agreste* (Zieger *et al.* 2008) as well as the aquatic limpets *Latia neritoides* and *Ancylus fluviatilis* (Meyer-Rochow and Bobkova 2001) where the sharp image lies well outside the retina. Although refractive power of the integument-cornea-complex is very significant in slugs, such shortening of the focal length of the two lenses still does not even allow a blurred image to be formed within the retina in the eyes of *A. rufus* and *D. agreste*.

The optics of the eyes in these pulmonates cannot assist in focusing an image on their shallow retinæ because to shorten the principal focal length of their lenses to place the focal point onto light-receiving layer would require a central refractive index of the lens of approximately 1.9 (Land 1981), which is well beyond that of even the densest crystalline proteins (Sweeney *et al.* 2007).

Such short offset of the lens and the retina seems to indicate that eyes in terrestrial snails and slugs as well as some aquatic limpets are not designed to receive a focused image and are likely to measure the average light intensity or quality over large angles rather than resolve fine image details.

Aquatic snails like *Lymnaea stagnalis*, *Radix peregra*, *Physa fontinalis*, and *Planorbarius corneus* are able to focus a sharp image on the light-receptive layer of the retina. It is due to the deepening of the latter, resulting in the increase of the vitreous body volume (Bobkova *et al.* 2004a, Gál *et al.* 2004).

Finally, it seems that there is no definite demarcation between lens eyes that form an image and those that do not. Nevertheless, we argue that it is the inappropriate geometry of the retina and the size of the eye in general, but not the optics alone, that cause the biggest differences between the eye designs in the species examined here.

VISUALLY MEDIATED BEHAVIOR

Visual capabilities and behavior

Numerous generalizations with regard to vision in pulmonate gastropods were based on observations of *Cornu aspersum aspersum* or closely related terrestrial snail species (Wheeler 1921, Geismer 1935, Zanforlin 1976, Bailey 1981, Hamilton and Winter 1984). Not surprisingly, a common assessment was that pulmonates have poor vision, *i.e.*, that their eyes can detect general light levels and perhaps broad areas of light and dark regions but not much else. However, comparisons of the visual capacities of freshwater snails and limpets, through behavioral tests and estimates based on analyses of eye structure and optics (Vakoliuk and Zhukov 2000, Meyer-Rochow and Bobkova 2001, Zhukov *et al.* 2002, Vakoliuk 2005), with those of terrestrial snails and slugs (Hermann 1968, Zhukov and Baikova 2001, Bobkova *et al.* 2004a, Gál *et al.* 2004, Vakoliuk 2005, Zieger *et al.* 2008) suggest a considerable range of visual capabilities exists within the pulmonate lineage.

Gastropods exhibit two easily distinguishable kinds of visual behavior. First, they can use light to orient by moving either toward, or more commonly, away from regions of high light intensity, and these responses usually take the form of a phototaxis. Second, gastropods may respond to a sudden decrease in light intensity by withdrawing into their shell and adhering tightly to the substratum. The first behavior is clearly concerned with habitat selection, while the second is a defense against a predator that casts a shadow prior to attack (Land 1968).

In pulmonates the ocular system (= paired cephalic eyes), but no other sensory system, is involved in the pho-

totactic behavioral response. This conclusion is the result of behavioral experiments with operated (eyeless) animals that did not show any sign of phototactic response, while intact molluscs did. Electrical recordings from the eye of *Lymnaea stagnalis* by Stoll and Bijlma (1973) gave only "on-responses", confirming that the shadow reflex was mediated by (1) dermal receptors, in *Nassarius reticulatus* (Linnaeus, 1758) according to Crisp (1972), (2) in the skin and along the mantle and in *L. stagnalis*, according to Stoll (1976), and (3) in the foot, lips, and tentacles as well.

The freshwater pulmonates *Lymnaea stagnalis* (Stoll 1972, 1973, 1976, Vakoliuk and Zhukov 2000) and *Planorbarius corneus* (Zhukov *et al.* 2002) clearly choose to move towards illuminated targets, displaying positive phototaxis. However, terrestrial pulmonate snails like *Cornu aspersum aspersum* (Wheeler 1921, Hamilton and Winter 1984), *Helix pomatia* (Geismer 1935), *Otala lactea* (Müller, 1774) (Hermann 1968), *Euparipha (Helix) pisana* (Müller, 1774) (Zanforlin 1976), *Achatina fulica* (Zhukov and Baikova 2001), *Cepaea nemoralis*, and *Trichia hispida* (Vakoliuk 2005) as well as the slugs *Agriolimax reticulatus* (Newell and Newell 1968), *Arion rufus*, and *Deroceras agreste* (Zieger *et al.* 2008) approach the dark regions of an experimental arena and, thus, display negative phototaxis.

A negative phototactic behavior is fully compatible with the dim or even dark environments that terrestrial snails and slugs are most active in (Newell and Newell 1968, Rollo and Wellington 1981, Hamilton and Winter 1984, Hommay *et al.* 1998, Cook 2001, Vakoliuk 2005). In contrast, positive phototaxis is compatible with the preference for a well-lit environment as, for example, in *Lymnaea stagnalis* and *Radix peregra* that exhibit moderately amphibious lifestyles and live on the algal growth of well-illuminated surfaces at the water/land boundary (Purchon 1977, Vakoliuk 2005).

Counsilman *et al.* (1987) suggested that in the bioluminescent terrestrial snail *Dyakia striata* (actually *Quantula striata* (Gray, 1834): Haneda 1981) the light produced by this species may have a social function. Although intraspecific communication by light was rejected by Meyer-Rochow and Moore (1988) for the bioluminescent freshwater pulmonate limpet *Latia neritoides*, comparisons of the eyes between this limpet and the equally large, but non-luminescent species *Ancylus fluviatilis* showed that the light-producing *Latia neritoides* had a significantly larger eye, larger lens, and more extensive retina (Meyer-Rochow and Bobkova 2001).

First described by Hamilton and Winter (1982), an experimental procedure to determine response thresholds for black stripes of different widths and orientation was then modified by Zhukov and Baikova (2001) and Vakoliuk (2005). Zhukov and Baikova (2001) have been able to show that the terrestrial snail *Achatina fulica* discriminates vertical and horizontal black stripes as well as grating patterns of

different frequencies. Discrimination tests revealed a strong preference for vertical bars over diagonal and horizontal bars of the same width in *Otala lactea* (Hermann 1968), a significant preference for horizontal bars over vertical ones in *Cepaea nemoralis* (Vakoliuk 2005), and no preference in *Lymnaea stagnalis*, *Planorbarius corneus* (Vakoliuk 2005), and *Cornu aspersum aspersum* (Hamilton and Winter 1984).

The experimentally determined resolution limits (Vakoliuk 2005) are well supported by our calculations of receptor spacings (for comparison in parentheses) (Gál *et al.* 2004) in *Lymnaea stagnalis*, *Planorbarius corneus*, *Cepaea nemoralis*, and *Trichia hispida*: 2.5°–5.7° (2.4°–5.2°), 1.4°–1.9° (1.4°–3.4°), 8.0° (8.0°), and >10.0° (13.0°). *Cornu aspersum aspersum* has a resolution limit of 14.5°–24.6° (Hamilton and Winter 1984) and *Otala lactea*, 0.9° for a single vertical bar and 2.4°–3.7° for a horizontal bar of similar dimensions (Hermann 1968).

However, we should keep in mind that behavioral response threshold estimates do not necessarily approximate actual sensory thresholds. Thus, our theoretically calculated performances of slug eyes show that a centrally-placed receptor subtends about 0.4° in *Arion rufus* and 4.7° in *Deroceras agreste*, so that acuity on purely anatomical grounds should be considered to be quite good in both species. Yet, behavioral tests show that these slugs do not respond until resolution thresholds of ca. 26° and ca. 90°, respectively, are reached (Zieger *et al.* 2008). The reasons for such disparity between anatomically-determined estimates and behaviorally-determined resolution limits are probably to be sought in features of either the visual processing or the optical system.

Our research has led us to conclude that anatomically the eyes of the two species of slugs investigated should be able to form images, but images that would lie in the wrong plane, well behind any retinal structures. The eyes of the slugs are designed to transmit spatially averaged intensity patterns of light and dark to the CNS for orientation and only one aspect of the visual environment, the overall pattern of light and dark, seems to be important for them. A sharp image is unnecessary and may even be a hindrance when the aim is to provide nothing more than orientation.

Newell and Newell (1968) estimated that two adjacent receptors subtend an angle of 15° at the center of the lens so that the visual acuity is poor in the eye of *Agriolimax reticulatus*. The authors presumed that the slug's eyes are adapted to detect changes in light intensity only and to operate at night.

Hamilton and Winter (1984) concluded that the poor vision of *Cornu aspersum aspersum* may correlate with primarily nocturnal habits. Geismer (1935) reported that in *Helix pomatia* a significant orientation response was released to a 24 × 20 cm black card of angular size extending at least

20° and positioned 25 cm away from the snail. According to Hermann (1968), another terrestrial snail, *Otala lactea*, can orient with respect to a target as small as 22.5°–30° at 25 cm distance. We have to conclude that the eye design in *Trichia hispida* and *Cepaea nemoralis* does not prevent image formation, but that resolution of the eyes can certainly not be great. Nevertheless, the eyes of these two snails are able to register not just the average light level but the quality of wide angles, and thus the crude direction, of a light source as well. This led us to suggest that the eye of terrestrial pulmonates, inherited from aquatic ancestors, has changed very little.

Secondarily aquatic pulmonates with higher visual needs are capable of image formation in both air and water. During their evolution, they have changed the terrestrial eye into a type that can function under water by deepening their retinæ, so that the latter are capable of handling the increase in focal length required for vision under water (Bobkova *et al.* 2004a, Gál *et al.* 2004).

CONCLUSION

The terrestrial snails *Cepaea nemoralis*, *Otala lactea*, *Coru aspersum aspersum*, *Achatina fulica*, and *Trichia hispida* are active under twilight conditions (*e.g.*, are crepuscular) and thus would need to be able to collect some light to be able to retain the image-forming ability of their eyes. Although their resolution is very poor, their eyes are able to register the average ambient light level as well as the quality of wide angles of light.

The slugs *Arion rufus* and *Deroceras agreste* are crepuscular but have high F-numbers of 8.5 and 2.5, respectively. It seems that the eyes of these gastropods have another visual task: they monitor environmental brightness and assist the animal in orientating towards dark places. The slugs simply do not need to perceive sharp images. The eyes of the limpets *Latia neritoides* and *Ancylus fluviatilis* also have no image-forming capacity, and the same conclusion as for the slugs may apply. However we do not know if the eyes of the limpets assist them in orienting towards dark, or toward light areas, and whether the somewhat larger eye of *L. neritoides* has something to do with the fact that this species can produce light when attacked (Meyer-Rochow and Moore 1988).

The eyes of *Lymnaea stagnalis* and *Radix peregra* are well adapted for vision in both watery and terrestrial habitats, and we suggest that the shape of the retina and the optics of the eyes of these snails match their amphibious life styles. The eyes of *Physa fontinalis* and *Planorbarius corneus* appear to have been less modified from those of their ancestors. Probably these snail species have lesser visual

needs and depend more on other senses like chemo- and mechanoreception.

Pulmonate gastropods use their eyes primarily for the following two kinds of visual task: (1) discriminating objects and possible enemies in their environment and (2) monitoring the environmental brightness level to orient towards dark places. The first type of visual task is characteristic of the aquatic snails and is served by image-forming eyes; the second is typical of terrestrial snails and slugs and is best served by a blurred image.

The studies on pulmonates can provide a more solid basis than currently exists for generalizations on the sensory capabilities of the molluscs in Class Gastropoda. Aside from the morphological and functional ramifications, this research is important from an evolutionary and taxonomic standpoint. The eyes are used as identifying characters in taxonomy or as a basis for comparisons in systematic discussions. An underlying knowledge of the function of the eyes, and why they take on a particular shape or design will obviously enhance their use or disuse as taxonomic or phylogenetic characters. Finally, an understanding of the various eye designs can shed light on evolutionary relationships and serve as a springboard for future research.

ACKNOWLEDGMENTS

Dr. M. Zieger wishes to thank members of UNITAS Malacologica and the National Science Foundation for support of her travels, and both authors express their gratitude to Dr. J. Serb for much good advice and encouragement. We are very grateful to our expert reviewers who gave us many useful suggestions.

LITERATURE CITED

- Aschenbrenner, S. and B. Waltz. 1998. Pleated septate junctions in leech photoreceptors: Ultrastructure, arrangement of septa, gate and fence function. *Cell and Tissue Research* **293**: 253-269.
- Baur, P. S., A. M. Brown, T. D. Rogers, and M. E. Brower. 1977. Lipochondria and the light response of *Aplysia* giant neurons. *Journal of Neurobiology* **8**: 19-42.
- Bailey, S. E. R. 1981. Circannual and circadian rhythms in the snail *Helix aspersa* Müller and the photoperiodic control of annual activity and reproduction. *Journal of Comparative Physiology* **142**: 89-94.
- Berg, E. V. 1978. Das Aktionsspektrum des Auges von *Helix pomatia* [Spectral sensitivity of the eyes of *Helix pomatia*]. *Zoologisches Jahrbuch für Physiologie* **82**: 483-492 [In German].
- Berg, E. V. and G. Schneider. 1967. Langsame Belichtungspotentiale der Augen von *Helix pomatia* L. [Slow light-induced potential from the eyes of *Helix pomatia* L.] *Naturwissenschaften* **54**: 591-592 [In German].
- Blumer, M. J. F. 1995. The ciliary photoreceptor in the teleplanic veliger-larvae of *Smargadina* sp. and *Strombus* sp. (Mollusca, Gastropoda). *Zoomorphology* **115**: 73-81.
- Bobkova, M. V. 1996. The form of the retina, structure of the lens and nature of the screening pigment in the eye of *Lymnaea stagnalis* L. *Journal of Evolutionary Biochemistry and Physiology* **32**: 95-97.
- Bobkova, M. B. 1998. Structural and functional organization of the peripheral part of the visual system of the common pond snail *Lymnaea stagnalis*. *Journal of Evolutionary Biochemistry and Physiology* **34**: 531-546.
- Bobkova, M. V., J. Gál, V. V. Zhukov, I. P. Shepeleva, and V. B. Meyer-Rochow. 2004a. Variations in the retinal designs of pulmonate snails (Mollusca, Gastropoda): Squaring phylogenetic background and ecophysiological needs (I). *Invertebrate Biology* **123**: 101-115.
- Bobkova, M. V., O. S. Tartakovskaya, S. L. Borissenko, V. V. Zhukov, and V. B. Meyer-Rochow. 2004b. Restoration of morphological and functional integrity in the regenerating eye of the giant African land snail *Achatina fulica*. *Acta Zoologica* **85**: 1-14.
- Brandenburger, J. L. 1975. Two new kinds of retinal cells in the eye of a snail, *Helix aspersa*. *Journal of Ultrastructural Research* **50**: 216-230.
- Brandenburger, J. L. and R. M. Eakin. 1970. Pathway of incorporation of vitamin A ³H₂ into photoreceptors of a snail, *Helix aspersa*. *Vision Research* **10**: 639-653.
- Brandenburger, J. L., R. M. Eakin, and C. T. Reed. 1976. Effect of light- and dark-adaptation on the photic microvilli and photic vesicles of the pulmonate snail *Helix aspersa*. *Vision Research* **16**: 1205-1210.
- Byzov, A. L. 1994. Эффективность синаптической передачи, управляемая морфологически, в фоторецепторах позвоночных и электрорецепторах ампул Лоренцини [Effectiveness of morphologically regulated synaptic transmission in vertebrate photoreceptors and electroreceptors of "Lorenzini Ampoules"] *Sensornie Systemi* **8**: 65-74 [In Russian].
- Chalazonitis, N. 1971. Transport macromoléculaire intraneuronique par vesicules (Neuropiled, *Helix*). [Transport of macromolecules by vesicles in the neurons (Neuropile, *Helix*).] *Comptes Rendus Hebdomadaires des Séances de Académie des Sciences* **273**: 1824-1827 [In French].
- Chase, R. 2002. *Behavior and its Neural Control in Gastropod Molluscs*. Oxford University Press, Inc. New York.
- Chernorizov, A. M., E. D. Shekhter, G. G. Arakelov, and M. M. Zimachev. 1994. The vision of the snail: The spectral sensitivity of the dark-adapted eye. *Neuroscience and Behavioral Physiology* **24**: 59-62.
- Cook, A. 2001. Behavioural ecology: On doing the right thing, in the right place at the right time. In: G. M. Barker, ed., *The Biology of Terrestrial Molluscs*. CAB International Publishing, New York. Pp. 447-487.
- Counsilman, J. J., D. Loh, S. Y. Chan, W. H. Tan, J. Copeland, and M. Maneri. 1987. Factors affecting the rate of flashing and loss

- of luminescence in an Asian land snail, *Dyakia striata*. *The Veliger* **29**: 394-399.
- Crisp, M. 1972. Photoreceptive function of an epithelial receptor in *Nassarius reticulatus* (Gastropoda). *Journal of the Marine Biological Association of the United Kingdom* **52**: 437-442.
- Demian, E. S. and F. Yousif. 1975. Embryonic development and organogenesis in the snail *Marisa cornuarietis* (Mesogastropoda: Ampullariidae). V. Development of the nervous system. *Malacologia* **15**: 29-42.
- Dennis, M. J. 1967. Electrophysiology of the visual system in a nudibranch mollusc. *Neurophysiology* **30**: 1434-1465.
- Eakin, R. M. 1963. Lines of evolution of photoreceptors. In: D. Mazia, and A. Tyler, eds., *General Physiology of Cell Specialization*. McGraw-Hill, New York. Pp. 393-425.
- Eakin, R. M. 1968. Evolution of photoreceptors. In: T. Dobzhansky, T. Hecht, and W. Steere, eds., *Evolutionary Biology*, Vol. 2. Appleton-Century-Crofts, New York. Pp. 194-242.
- Eakin, R. M. 1972. Structure of invertebrate photoreceptors. In: H. J. A. Darnall, ed., *Handbook of Sensory Physiology*, Vol. VII/1. Springer-Verlag, Berlin, Heidelberg, New York. Pp. 625-684.
- Eakin, R. M. 1990. Photic vesicles. *The Veliger* **33**: 209-214.
- Eakin, R. M. and J. L. Brandenburger. 1967a. Differentiation in the eye of a pulmonate snail *Helix aspersa*. *Journal of Ultrastructural Research* **18**: 391-421.
- Eakin, R. M. and J. L. Brandenburger. 1967b. Vesicles and granules in the retina of a snail, *Helix aspersa*. *25th Annual Meeting, Electron Microscopy Society of America, Chicago*. Claitor's Book Store, Baton Rouge, Louisiana. Pp. 212-213.
- Eakin, R. M. and J. L. Brandenburger. 1970. Osmic staining of amphibian and gastropod photoreceptors. *Journal of Ultrastructural Research* **30**: 619-641.
- Eakin, R. M. and J. L. Brandenburger. 1972. Structural basis for pulsations in the eye of a snail, *Helix aspersa*. *30th Annual Meeting, Electron Microscopy Society of America, Los Angeles*. Claitor's Book Store, Baton Rouge, Louisiana. Pp. 46-47.
- Eakin, R. M. and J. L. Brandenburger. 1975a. Understanding a snail's eye at a snail's pace. *American Zoologist* **15**: 851-863.
- Eakin, R. M. and J. L. Brandenburger. 1975b. Retinal differences between light-tolerant and light-avoiding slugs (Mollusca: Pulmonata). *Journal of Ultrastructural Research* **53**: 382-394.
- Eakin, R. M. and J. L. Brandenburger. 1982. Pinocytosis in eyes of a snail, *Helix aspersa*. *Journal of Ultrastructural Research* **80**: 214-229.
- Eakin, R. M., J. L. Brandenburger, and G. M. Barker. 1980. Fine structure of the eye of the New Zealand slug, *Athoracophorus bitentaculatus*. *Zoomorphology* **94**: 225-239.
- Eakin, R. M. and M. M. Ferlatte. 1973. Studies on eye regeneration in a snail, *Helix aspersa*. *Journal of Experimental Zoology* **184**: 81-95.
- Eskin, A. and E. Harcombe. 1977. Eye of *Navanax*: Optic activity, circadian rhythm and morphology. *Comparative Biochemistry and Physiology* **57A**: 443-449.
- Flari, V. and H. Lasaridou-Dimitriadou. 1995. The impact of nocturnal light pulses on the activity pattern of terrestrial snails (*Helix lucorum*) entrained to photoperiod of 12h light: 12h dark. *Canadian Journal of Zoology* **73**: 1214-1220.
- Ford, D. J. G. and A. Cook. 1988. Responses to pulsed stimuli in a pulmonate slug (*Limax pseudoflavus*). *Journal of Zoology* **214**: 663-672.
- Ford, D. J. G. and A. Cook. 1994. The modulation of rhythmic behaviour in the pulmonate slug *Limax pseudoflavus* by season and photoperiod. *Journal of Zoology* **232**: 419-434.
- Gál, J., M. V. Bobkova, V. V. Zhukov, I. P. Shepeleva, and V. B. Meyer-Rochow. 2004. Fixed focal-length optics in pulmonate snails (Mollusca, Gastropoda): Squaring phylogenetic background and ecophysiological needs (II). *Invertebrate Biology* **123**: 116-127.
- Geisner, A. 1935. Die lokomotorischen Reaktionen von *Helix pomatia* auf Helligkeit und Dunkelheit und der Einfluss von Eingriffen an augen und Zentralnervensystem [Locomotor reactions of *Helix pomatia* to light and darkness and influence of interventions to the eyes and nervous system]. *Zoologische Jahrbücher. Abteilung für allgemeine Zoologie und Physiologie der Tiere* **55**: 95-130 [In German].
- Gillary, H. L. 1970. Electrical responses from the eye of *Helix* to photic stimulation and simultaneous electrical stimulation of the optic nerve. *Vision Research* **10**: 977-991.
- Gillary, H. L. 1974. Light-evoked electrical potentials from the eye and optic nerve of *Strombus*: Response waveform and spectral sensitivity. *Journal of Experimental Biology* **60**: 383-396.
- Gillary, H. L. and M. L. Wolbarsht. 1967. Electrical responses from the eye of a land snail. *Revue Canadienne de Biologie* **26**: 125-134.
- Grassé, P. P. 1948. *Traité de Zoologie [Treatise on Zoology]*, Book 5, Vol. 3. Masson et cie, Paris [In French].
- Hamilton, P. V. and M. A. Winter. 1982. Behavioural responses to visual stimuli by the snail *Littorina irrorata*. *Animal Behaviour* **30**: 752-760.
- Hamilton, P. V. and M. A. Winter. 1984. Behavioural responses to visual stimuli by the snails *Tectarius muricatus*, *Turbo castanea*, and *Helix aspersa*. *Animal Behaviour* **32**: 51-57.
- Hamilton, P. V., S. C. Ardizzoni, and J. S. Penn. 1983. Eye structure and optics in the intertidal snail *Littorina irrorata*. *Journal of Comparative Physiology* **152A**: 435-445.
- Haneda, Y. 1981. Luminescence activity of the land snail *Quantula striata*. *Bioluminescence and Chemiluminescence* **19**: 257-265.
- Hara, T., R. Hara, and J. Takeuchi. 1967. Rhodopsin and retinochrome in the octopus retina. *Nature* **214**: 572-573.
- Hermann, H. T. 1968. Optic guidance of locomotor behavior in the land snail, *Otala lactea*. *Vision Research* **8**: 601-612.
- Henchman, A. P. 1897. The eyes of *Limax maximus*. *Science* **5**: 428-429.
- Hodasi, J. K. M. 1982. The effects of different light regimes on the behaviour and biology of *Achatina (Achatina) achatina* (Linné). *Journal of Molluscan Studies* **48**: 283-293.
- Hommay, G., O. Lorgelec, and F. Jacky. 1998. Daily activity rhythm and use of shelter in the slugs *Deroceras reticulatum* and *Arion distinctus* under laboratory conditions. *Annals of Applied Biology* **132**: 167-185.
- Hughes, H. P. I. 1970. The spectral sensitivity and absolute threshold of *Onchidoris fusca* (Müller). *Journal of Experimental Biology* **52**: 609-618.

- Jeppesen, L. L. 1977. Photoperiodic control of hibernation in *Helix pomatia* L. (Gastropoda: Pulmonata). *Behavioural Processes* 2: 373-382.
- Kashiwagi, T., V. B. Meyer-Rochow, K. Nishimura, and E. Eguchi. 1997. Fatty acid composition and ultrastructure of photoreceptive membrane in the crayfish *Procambarus clarkii* under conditions of thermal and photic stress. *Journal of Comparative Physiology* 167B: 1-8.
- Kashiwagi, T., V. B. Meyer-Rochow, K. Nishimura, and E. Eguchi. 2000. Light activation of phospholipase A2 in the photoreceptor of the crayfish *Procambarus clarkii*. *Acta Neurobiologiae Applicata et Experimentalis* 60: 9-16.
- Katagiri, N. and Y. Katagiri. 1998. Fine structure of the dioptric apparatus in the stalk eye of *Onchidium verruculatum* (Gastropoda, Stylomatophora): A distinct lamellar substructure of the lens. *Zoomorphology* 118: 13-21.
- Katagiri, N., Y. Katagiri, Y. Shimatani, and Y. Hashimoto. 1995. Cell type and fine structure of the retina of *Onchidium* stalk-eye. *Journal of Electron Microscopy* 44: 219-230.
- Katagiri, N., A. Terakita, Y. Shichida, and Y. Katagiri. 2001. Demonstration of a rhodopsin-retinochrome system in the stalk eye of a marine gastropod, *Onchidium*, by immunohistochemistry. *Journal of Comparative Neurology* 433: 380-389.
- Katagiri, N., T. Y. Suzuki, Y. Shimatani, and Y. Katagiri. 2002. Localization of retinal proteins in the stalk and dorsal eyes of the marine gastropod, *Onchidium*. *Zoological Science* 19: 1231-1240.
- Kataoka, S. 1975. Fine structure of the retina of a slug, *Limax flavus* L. *Vision Research* 75: 681-686.
- Kataoka, S. 1977. Ultrastructure of the cornea and accessory retina in a slug, *Limax flavus* L. *Journal of Ultrastructural Research* 60: 296-305.
- Kerkut, G. A. and R. J. Walker. 1975. Nervous system, eye and statocyst. In: V. Fretter and J. Peake, eds., *Pulmonates. I. Anatomy and Physiology*. Academic Press, London. Pp. 165-244.
- Land, M. F. 1968. Functional aspects of the optical and retinal organization of the mollusc eye. *Symposia of the Zoological Society of London* 23: 75-96.
- Land, M. F. 1981. Optics and vision in invertebrates. In: H. J. Autrum, ed., *Handbook of Sensory Physiology* Vol. 6B. Springer, Berlin-Heidelberg, New York. Pp. 471-592.
- Land, M. F. 1984. Molluscs. In: M. A. Ali, ed., *Photoreception and Vision in Invertebrates*, Plenum Publishing Corporation, New York. Pp. 699-725.
- Land, M. F. and R. D. Fernald. 1992. The evolution of eyes. *Annual Review of Neuroscience* 15: 1-29.
- Land, M. F. and D.-E. Nilsson. 2002. *Animal Eyes*. Oxford University Press, Oxford, U.K.
- Lewis, R. D. 1969. Studies on the locomotor activity of the slug *Arion ater* (Linnaeus). I. Humidity, temperature and light reactions. *Malacologia* 7: 295-306.
- Matthiessen, L. 1886. Über den physikalisch-optischen Bau des Auges der Cetaceen und der Fische [On physical and optical of the eyes in cetacean and fishes]. *Pflügers Archiv* 38: 521-528 [In German].
- Messenger, J. B. 1981. Comparative physiology of vision in molluscs. In: H. J. Autrum, ed., *Handbook of Sensory Physiology*, Vol. VII/6C. Springer, Berlin. Pp. 93-200.
- Messenger, J. B. 1991. Photoreception and vision in molluscs. In: J. R. Cronly-Dillon and R. L. Gregory, eds., *Vision and Visual Disfunction*, Vol. 2. Macmillan, Basingstoke, UK. Pp. 364-397.
- Meyer-Rochow, V. B. 1994. Light-induced damage to photoreceptors of spiny lobsters and other crustaceans. *Crustaceana* 67: 97-111.
- Meyer-Rochow, V. B. 2001. The crustacean eye: Dark/light adaptation, polarization sensitivity, flicker fusion frequency, and photoreceptor damage. *Zoological Science* 18: 1175-1197.
- Meyer-Rochow, V. B. and M. V. Bobkova. 2001. Anatomical and ultrastructural comparisons between the eyes of two species of aquatic, pulmonate gastropods: The bioluminescent *Latia neritoides* (Gray, 1850) and the non-luminescent *Ancylus fluviatilis* (Müller, 1774). *New Zealand Journal of Marine and Freshwater Research* 35: 739-750.
- Meyer-Rochow, V. B. and S. Moore. 1988. Biology of *Latia neritoides* Gray 1850 (Gastropoda, Pulmonata, Basommatophora): The only light-producing freshwater snail in the world. *International Review der Gesamten Hydrobiologie* 73: 21-42.
- Meyer-Rochow, V. B., T. Kashiwagi, and E. Eguchi. 2002. Selective photoreceptor damage in four species of insects induced by experimental exposures to UV-irradiation. *Micron* 33: 23-31.
- Mortensen, C. and R. M. Eakin. 1974. Efferent neuritis to capsular muscles in the eye of a snail, *Helix aspersa*. *Journal of Ultrastructural Research* 49: 286-294.
- Nasi, E., M. del Pilar Gomez, and R. Payne. 2000. Phototransduction mechanism in microvillar and ciliary photoreceptors of invertebrates. In: D. G. Stavenga, W. J. Degrip, and E. N. Pugh, eds., *Handbook of Biological Physics*, Vol. 3. Elsevier, Amsterdam. Pp. 389-448.
- Newell, P. F. and G. E. Newell. 1968. The eye of the slug, *Agriolimax reticulatus* (Müll.) *Symposia of the Zoological Society of London* 23: 97-111.
- Nilsson, D.-E. 1989. Optics and evolution of the compound eye. In: D. G. Stavenga and R. C. Hardie, eds., *Facets of Vision*. Springer, Berlin. Pp. 30-73.
- Nilsson, D.-E., M. F. Land, and J. Howard. 1988. Optics of the butterfly eye. *Journal of Comparative Physiology* 161A: 645-658.
- Oswaldo-Cruz, E. and R. E. Bernardes. 1982. Morphological and functional observations on the eye of *Strophochelius* (Mollusca, Gastropoda, Stylomatophora). *Brazilian Journal of Medical and Biological Research* 15: 161-174.
- Ozaki, K., R. Hara, and T. Hara. 1983. Histochemical localization of retinochrome and rhodopsin studied by fluorescence microscopy. *Cell Tissue Research* 233: 335-345.
- Pasic, M., D. Zecevic, D. Ristanovic, and G. Popilijevic. 1974. Effect of intermittently applied light on *Helix pomatia* neurons. *Comparative Biochemistry and Physiology* 51A: 71-74.
- Purchon, R. D. 1977. *The Biology of Mollusca*. Pergamon Press, Oxford, U.K.
- Rollo, C. D. and W. G. Wellington. 1981. Environmental orienta-

- tion by terrestrial Mollusca with particular reference to homing behavior. *Canadian Journal of Zoology* **59**: 225-239.
- Röhlich, P. and J. J. Török. 1963. Die Feinstruktur des Auges der Weinbergschnecke (*Helix pomatia* L.) [Ultrastructure of the eyes in the grape snail (*Helix pomatia* L.)]. *Zeitschrift für Zellforschung und mikroskopische Anatomie* **60**: 348-368 [In German].
- Sakakibara, M. 2006. Comparative study of visuo-vestibular conditioning in *Lymnaea stagnalis*. *Biological Bulletin* **210**: 298-307.
- Salwini-Plawen, L. v. and E. Mayr. 1977. On the evolution of photoreceptors and eyes. *Evolutionary Biology* **10**: 207-263.
- Schwalbach, G., K. G. Lickfeld, and M. Hahn. 1963. Der mikromorphologische Aufbau des Linsenauges der Weinbergschnecke (*Helix pomatia* L.). [Micromorphological structure of the lens eyes of the grape snail (*Helix pomatia* L.)] *Protoplasma* **56**: 242-273 [In German].
- Segal, E. 1960. In: *Discussion following paper by A. J. Marshall. Cold Spring Harbor Symposium on Quantitative Biology* **25**: 504-505.
- Seyer, J.-O. 1992. Resolution and sensitivity in the eye of the winkle *Littorina littorea*. *Journal of Experimental Biology* **170**: 57-69.
- Seyer, J.-O. 1994. Structure and optics of the eye in hawk-wing conch *Strombus raninus* (L.) *Journal of Experimental Zoology* **268**: 200-207.
- Seyer, J.-O., D.-E. Nilsson, and E. J. Warrant. 1998. Spatial vision in the prosobranch gastropod *Ampularia* sp. *Journal of Experimental Biology* **201**: 1673-1679.
- Stoll, C. J. 1972. Sensory systems involved in the shadow response of *Lymnaea stagnalis*. *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen* **75C**: 342-351.
- Stoll, C. J. 1973. On the role of eyes and non-ocular light receptors in orientational behaviour of *Lymnaea stagnalis*. *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen* **76C**: 204-214.
- Stoll, C. J. 1976. Extraocular photoreception in *Lymnaea stagnalis* (L.). In: J. Sálanki, ed., *Neurobiology of Invertebrates: Gastropoda Brain*, Tihany 1975, Akadémiai Kiadó, Budapest. Pp. 487-495.
- Stoll, C. J. and A. Bijlma. 1973. Optic nerve responses in *Lymnaea stagnalis* (L.) (Pulmonata, Basommatophora) to photic stimulation of the eye. *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen* **76C**: 1-8.
- Strumwasser, F., R. B. Alvarez, D. P. Viele, and J. C. Wolum. 1979. Structure and function of a neuronal circadian oscillator. In: M. Suda, O. Hayaishi, and H. Nakagawa, eds., *Biological Rhythms and Their Central Mechanisms*. Elsevier/North-Holland Biomedical Press, Amsterdam. Pp. 51-56.
- Suzuki, H., M. Watanabe, Y. Tsukahara, and K. Tasaki. 1979. Duplex system in the simple retina of a gastropod mollusc, *Limax flavus* L. *Journal of Comparative Physiology* **133**: 125-130.
- Sweeney, A. M., D. L. Des Marais, Y. E. Ban, and S. Johnsen. 2007. Evolution of graded refractive index in squid lenses. *Journal of the Royal Society, Interface* **4**: 685-698.
- Tamamaki, N. 1989. The accessory photosensory organ of the terrestrial slug, *Limax flavus* L. (Gastropoda, Pulmonata): Morphological and electrophysiological study. *Zoological Science* **6**: 877-883.
- Tamamaki, N., and K. Kawai. 1983. Ultrastructure of the accessory eye of the giant snail, *Achatina fulica* (Gastropoda, Pulmonata). *Zoomorphology* **102**: 205-213.
- Terakita, A., R. Hara, and T. Hara. 1989. Retinal-binding protein as a shuttle for retinal in the rhodopsin-retinochrome system of the squid visual cells. *Vision Research* **29**: 639-652.
- Tomarev, S. I. and J. Piatigorsky. 1996. Lens crystalins of invertebrates—diversity and recruitment from detoxification enzymes and novel proteins. *European Journal of Biochemistry* **235**: 449-465.
- Vakoliuk, I. A. 2005. Сравнительное исследование зрения брюхоногих легочных моллюсков на основе фотоориентационного поведения [Comparative studies of vision in gastropod pulmonates based on light-orientational behavior]. Ph.D. Dissertation, Immanuel Kant State University, Kaliningrad, Russia [In Russian].
- Vakoliuk, I. A. and V. V. Zhukov. 2000. Photoreception in *Lymnaea stagnalis* based on phototaxis data. *Journal of Evolutionary Biochemistry and Physiology* **36**: 419-423.
- Vanfleteren, J. R. 1982. A monophyletic line of evolution? Ciliary induced photoreceptor membranes. In: J. A. Westfall, ed., *Visual Cells in Evolution*. Raven Press, New York. Pp. 107-136.
- Walls, G. Y. 1942. The vertebrate eye and its adaptive radiation. *Bulletin of Crenbrook Institute of Science* **19**: 1-785.
- Warrant, E. J. and P. D. McIntyre. 1993. Arthropod eye design and the physical limits to special resolving power. *Progress in Neurobiology* **40**: 413-461.
- Warrant, E. and D.-E. Nilsson. 2006. *Invertebrate Vision*. Cambridge University Press, Cambridge, U.K.
- Willem, V. 1892. Contributions à l'étude physiologique des organes de sens chez les mollusques. I. La vision chez les gastropodes pulmonés. [On the studies of physiology of sensory organs in mollusks. I. Vision in pulmonate gastropods]. *Archives de Biologie* **12**: 5-125 [In French].
- Wheeler, V. 1921. The phototropism of land snails. *Journal of Comparative Psychology* **1**: 149-154.
- Whitmore, D., and G. D. Block. 1996. Cellular aspects of molluscan biochronometry. *Seminars in Cell and Developmental Biology* **7**: 781-789.
- Whittle, A. C. 1976. Reticular specializations in photoreceptors: A review. *Zoologica Scripta* **5**: 191-206.
- Zanforlin, M. 1976. Observations on the visual perception of the snail *Euparipha pisana* (Müller). *Bollettino di Zoologia* **43**: 303-315.
- Zieger, M. V., I. A. Vakoliuk, O. P. Tuchina, V. V. Zhukov, and V. B. Meyer-Rochow. 2008. Eyes and vision in *Arion rufus* and *Deroceras agreste* (Mollusca; Gastropoda; Pulmonata): What role does photoreception play in the orientation of these terrestrial slugs? *Acta Zoologica* **89**: in press.
- Zhukov, V. V. and I. B. Baikova. 2001. Влияние зрительных стимулов на выбор направления движения у *Achatina fulica* [Influence of visual stimuli upon the choice of motive directions in *Achatina fulica*. *Sensornie Systemi* **15**: 136-142 [in Russian].

- Zhukov, V. V. and F. G. Gribakin. 1990. Спектральная чувствительность глаз моллюсков *Lymnaea stagnalis* L. и *Planorbarius corneus* L. в ультрафиолетовой и видимой частях спектра [Spectral sensitivity of the eyes in mollusks *Lymnaea stagnalis* L. and *Planorbarius corneus* L. in ultraviolet and visible spectrum regions]. *Sensornie Systemi* 4: 341-142.
- Zhukov, V. V. and O. P. Tuchina. 2008. Структура зрительных путей в нервной системе пресноводных легочных моллюсков *Lymnaea stagnalis* и *Planorbarius corneus* [Structure of visual pathways in the nervous system of freshwater pulmonate molluscs *Lymnaea stagnalis*, and *Planorbarius corneus*]. *Journal of Evolutionary Biochemistry and Physiology* 40: 291-301 [in Russian].
- Zhukov, V. V., M. B. Bobkova, and I. A. Vakoliuk. 2002. Eye structure and vision in the freshwater pulmonate mollusc *Planorbarius corneus*. *Journal of Evolutionary Biochemistry and Physiology* 38: 41-430.
- Zhukov, V. V., N. L. Kononenko, I. B. Paramonov, and S. L. Borisenko. 2006. Серотонин изменяет электрические реакции глаза *Lymnaea stagnalis* на световую стимуляцию [Serotonin changes the electrical responses of the eye to light in *Lymnaea stagnalis*]. *Sensornie Systemi* 20: 270-278 [In Russian].
- Zunke, V. 1979. Ultrastructure of the eye of the amber snail *Succinea putris* (L.) (Gastropoda, Stylommatophora). *Malacologia* 18: 1-5.

Submitted: 26 October 2007; **accepted:** 21 August 2008;
final revisions received: 13 October 2008